

10.—*Blinasaurus*, a brachyopid genus from Western Australia and New South Wales

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Abstract

A new genus, *Blinasaurus*, is proposed for two brachyopid species occurring in Triassic deposits of Australia. The type species, *Platyceps wilkinsoni* Stephens, 1887, from the Lower to Middle Triassic Gosford Formation of New South Wales, is based on a single incomplete skeleton. The second species, *B. henwoodi*, from the basal Triassic Blina Shale, of Western Australia, is known from a holotype skull and an assortment of paratypic skull fragments, lower jaws and clavicles. The genus is compared with the brachyopid species *Batrachosuchus browni*, *B. watsoni*, *Bothriceps australis*, *Brachyops laticeps* and *Trucheosaurus major*. *Boreosaurus thorslundi* and *Hadrokkosaurus bradyi* are added to the family. *Tungusso-gyrinus bergi* and *Indobrachyops panchetensis* are excluded from the Brachyopoidea and *Tupilakosaurus wetlugensis* from the Brachyopidae. Evolutionary trends in the family and the stratigraphic occurrences of the various species are considered.

Introduction

Blinasaurus wilkinsoni (Stephens, 1887) is based on a single specimen of a larval brachyopid consisting of a skull roof, branchial bars and part of the postcranial skeleton. The species is one of two temnospondyls associated with a large fish assemblage recovered from a quarry in the Lower Triassic Gosford Formation near Gosford, New South Wales. The other temnospondyl is a new undescribed species of the capitosaurid genus, *Parotosaurus*. The fish assemblage was originally described by Woodward (1890) and later revised by Wade (1940).

Blinasaurus henwoodi occurs in the upper part of the Blina Shale of the Fitzroy Trough in the West Kimberley District, Western Australia. It is associated at several fossil localities with *Deltasaurus kimberleyensis* (see Cosgriff, 1965) and with additional undescribed vertebrate material which includes a capitosaurid, two trematosaurids, a coelacanth, *Ceratodus* and *Saurichthys*.

The first collection of vertebrate fossils from the Blina Shale was made at Dry Corner syncline in 1953 by a field party of the Bureau of Mineral Resources (see Brunnschweiler, 1954). A large amount of vertebrate material was collected in June and July, 1960, from Erskine Range exposures, U.C.M.P. localities V6040, V6041, V6042 and V6043 and from a hill on Calwinyardah station, U.C.M.P. V6044 by a joint field party of the Western Australian Museum and the University of California, Berkeley. The holotypic skull described below was found by Dr. W. D. L. Ride at U.C.M.P. V6041 during this trip. The nature and location of these localities is given in a following section.

More paratypic material of *Blinasaurus henwoodi* and *Deltasaurus kimberleyensis* was recovered from the surface and from several

quarries at V6040 by Dr. Ride in July, 1963, by Mr. E. J. Car in August, 1963, by Mr. D. Merrilees and Dr. E. H. Colbert in May, 1964, and by Mr. Merrilees again in August, 1964. Dr. J. W. Warren and the author collected at several of the localities in June and July, 1965, during a field trip of the Department of Zoology and Comparative Physiology, Monash University, led by Professor A. J. Marshall. Additional paratypic material of *Blinasaurus henwoodi*, *Deltasaurus kimberleyensis*, *Ceratodus* and *Saurichthys* was recovered from the surface and quarries at V6040, of *D. kimberleyensis* from the quarry at V6043 and of *D. kimberleyensis*, *B. henwoodi*, one of the trematosaurids and an unidentified actinopterygian from the surface at V6044.

The genus is also represented in Lower Triassic deposits of Tasmania by a third species, undescribed as yet. This species, closely related to both *B. wilkinsoni* and *B. henwoodi*, is present in a number of fossil assemblages collected from exposures of the Knocklofty Formation in the southeastern part of the island by the author and other persons during the years 1964-1967. It is known from an abundance of material, including several complete and partial skulls, many skull and lower jaw fragments, dermal shoulder girdle elements and an assortment of limb bones. Faunal associates of *Blinasaurus* sp. in these assemblages include *Deltasaurus kimberleyensis*, a new genus and species of the Rhytidosteidae, a lydekkerinid, a chasmatosaurid reptile, *Ceratodus*, *Cleithrolepis* and *Saurichthys*.

A variety of stratigraphic evidence, summarised in a subsequent section of this paper indicates that the fauna of the Knocklofty Formation is nearly contemporary with the fauna of the Blina Shale and that both lie at the very base of the Triassic. Other evidence, however, suggests that the fauna of the Gosford Formation is stratigraphically higher than that of the Western Australian and Tasmanian faunas and that its position may be Middle Triassic.

Abbreviations used in the text

Various fossil specimens are referred to by number in the descriptive and comparative passages below. The abbreviations which precede these numbers denote institutions as follows: B.M.N.H.: British Museum (Natural History); N.S.W.G.S.: Mining Museum of the New South Wales Geological Survey; S.M.N.H.: Swedish Museum of Natural History; U.C.M.P.: Museum of Paleontology, University of California, Berkeley; U.I.P.: Paleontological Institute of the University of Uppsala; U.T.G.D.: Geology Department of the University of Tasmania; W.A.M.: Western Australian Museum.

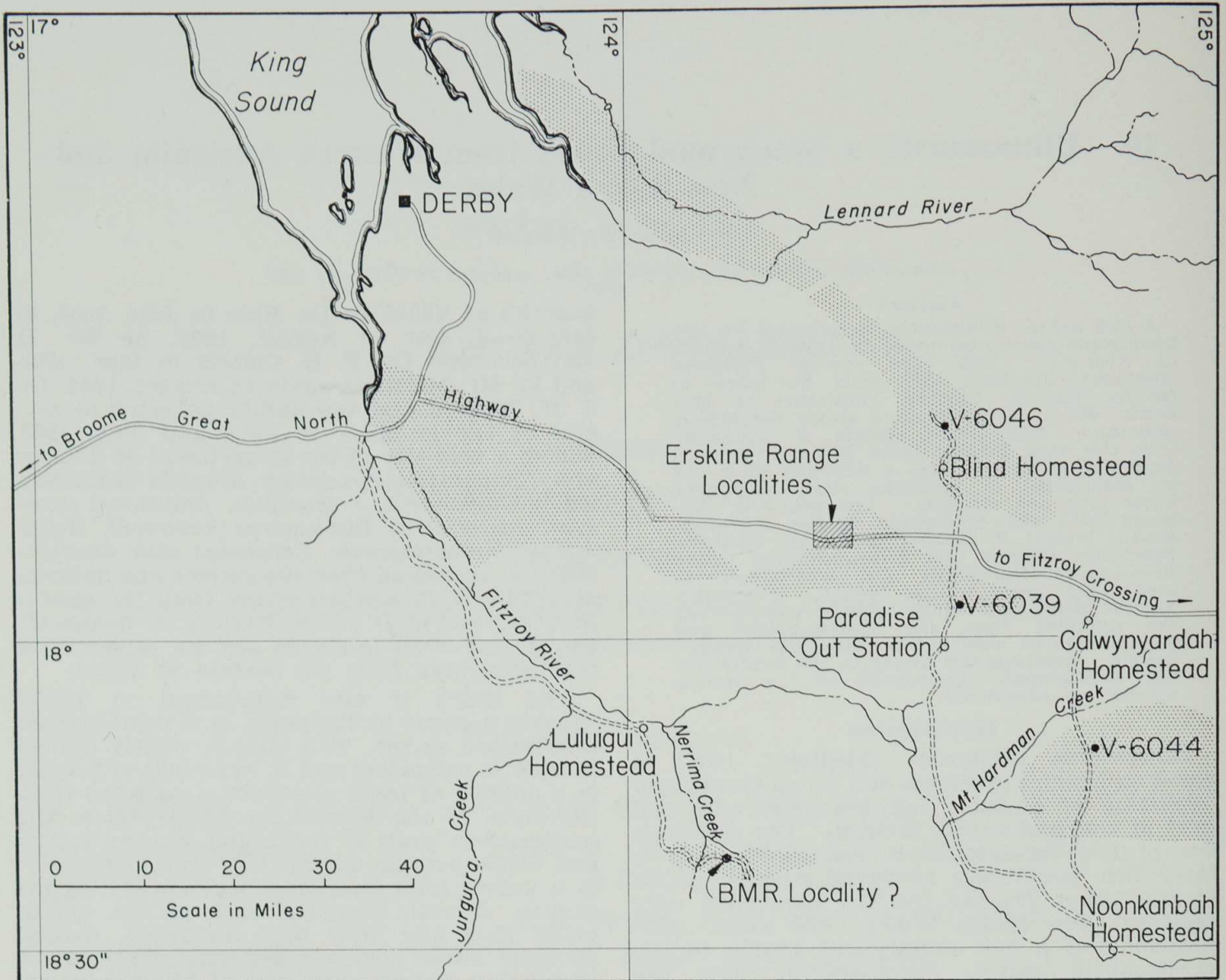


Figure 1.—A portion of the West Kimberley District of Western Australia, showing outcrops of the Blina Shale (stippling) and the fossil vertebrate localities. Most of this map is based on the solid geology sheet of the Fitzroy Basin compiled by S. D. Henderson and included in Guppy et. al. (1958).

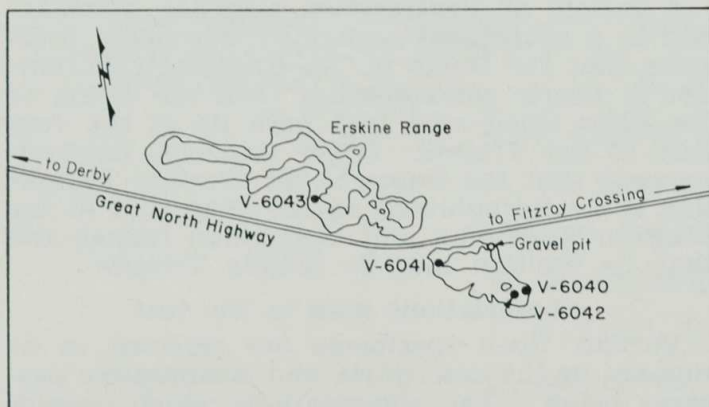


Figure 2.—The Erskinie Range localities. This map is an enlargement of the hatched area shown on Figure 1.

Fossil vertebrate localities in the Blina Shale

The fossil localities shown on Figures 1 and 2, with the exception of the B.M.R. locality, are designated by University of California Museum of Paleontology numbers. The B.M.R. locality is a site where a Bureau of Mineral Resources field party collected vertebrate fossils in 1953.

The field notes pertaining to this were destroyed in a fire and the exact location has not been re-established. (See Cosgriff, 1965, p. 67).

McKenzie (1961) mapped the fossiliferous localities and investigated the stratigraphy. His report includes a synopsis of the field work, detailed descriptions of the lithology and an analysis of the depositional environment. The U.C.M.P. locality numbers cited in this article correspond to the localities of McKenzie as follows:

- U.C.M.P. locality V6040=McKenzie, fig. 1, p. 70, locality 4 (quarries 1, 2 and 3);
- U.C.M.P. locality V6041=McKenzie, fig. 1, p. 70, locality 6;
- U.C.M.P. locality V6043=McKenzie, fig. 1, p. 70, locality 8;
- U.C.M.P. locality V6046=McKenzie, Table II, p. 73, first entry ("Between Bannons and Mimosa Bores. Blina Station; 124° 31' E., 17° 40' S.").

The fossil localities divide into two geographic categories. The first of these, the outlying localities, is shown on Figure 1. The other, the Erskinie Range localities, is shown on Figure 2 which is an enlargement of the hatched area on Figure 1. Each of these maps shows some of

the localities listed above as well as others which are not relevant to this article as they have not produced fossils of *Blinasaurus henwoodi*. Most of these latter, however, have produced fossils of *Deltasaurus kimberleyensis* and locality descriptions and finding directions are given in the previous article on this taxon (Cosgriff, 1965). V6046 is the only locality of the outlying group which is known to contain *Blinasaurus henwoodi*. To reach this locality drive 3 miles north from Blina Homestead on the station road to Bannan's Bore. Then drive 8.2 miles farther north from Bannan's Bore on the road to Mimosa Bore. The locality is a low topographic rise about 20 yards east of the road.

The Erskine Range, a series of low mesas, lies about 69 miles east of Derby on the Great North Highway. Two of the localities, V6040 and V6041, lie south of the Highway and the other, V6043, is north of the Highway on the principal Mesa. V6040 is on the south slope of a small rounded hill which differs from the other portions of the range in lacking a capping of Erskine Sandstone. V6041 is on the north side of the Mesa south of the highway about half-way up the slope from the Mesa foot to the Blina Shale-Erskine Sandstone contact. V6043 is near the foot of the south face of the principal Mesa.

Superfamily Brachyopoidea

The superfamily, as considered in this report, contains only the families Brachyopidae and Dvinosauridae. Watson (1956) has reaffirmed the close relationship of *Dvinosaurus* to the Brachyopidae. The genus, included in the family by von Huene (1922 and 1948), Efremov (1928 and 1932), Sushkin (1936) and Bystrov (1938), seems distinctive enough to warrant family separation. The family Dvinosauridae was originally proposed by Säve-Söderbergh (1935) but was placed by him in a separate superfamily, the Dvinosauroidae.

Diagnosis. The diagnostic characters are principally those given by Watson (1919 and 1956) for the family Brachyopidae. Skull broad and parabolic. Orbits in anterior part of skull roof. Otic notch absent or rudimentary. Orbital and antorbital regions of the skull relatively shallow. Cheek deep. Palate highly vaulted in occipital aspect. Occipital portions of the squamosal and quadratojugal concave in posterior view. Long narrow fissure between the squamosal and the pterygoid.

In addition, the following feature of the lower jaw construction is uniform through all species of the superfamily for which the lower jaw is known: posterior meckelian foramen and angular-prearticular suture on ventral surface or very low on lingual surface.

Family Dvinosauridae

Diagnosis. Occipital condyles directly beneath the posterior edge of the skull roof. Basicranial joints present between the basisphenoid and pterygoid bones; pterygoid bones not joined by suture to parasphenoid bone. Palatal tooth row present on ectopterygoid and palatine bones as well as on vomer bones.

Family Brachyopidae

Diagnosis. Occipital condyles far behind the posterior edge of the skull roof. Basicranial joints absent; pterygoid bones joined by suture to parasphenoid bones. Palatal tooth present only on vomer bones.

Blinasaurus ¹Romer, 1966, p. 363 [nom. nud.]²
Type species. *Platyceps wilkinsoni* Stephens, 1887, p. 1175, pl. 22. Upper part of Gosford Formation, Narrabeen Group. Gosford, New South Wales. Middle Triassic.

Differential diagnosis. Strictly definitive characters to distinguish *Blinasaurus* from the other genera of the family are entirely lacking, necessitating a differential diagnosis. The other genera are listed below together with the important characters by which each is distinguished from *Blinasaurus*. The characters concerned with the position of the orbits on the skull roof and the size of the adductor fossa are quantitative and the indices on which they are based are given in Table I.

Bothriceps and *Trucheosaurus*. The skull roofs are roughly triangular in dorsal view whereas that of *Blinasaurus* is nearly circular. The antorbital portions of the skull roofs are relatively longer: in each of these genera the portion of the skull roof anterior to the orbits, as measured on the midline, is about one-third of the total midline length of the skull roof; in *Blinasaurus* it is about one-quarter.

Brachyops. The snout is slightly pointed in dorsal view; in *Blinasaurus* it is evenly rounded. The orbits are more widely spaced, the least interorbital width being between one-third and a half of skull roof midline length; in *Blinasaurus* it is between a quarter and a third.

Batrachosuchus. The orbits are more widely spaced than in *Blinasaurus*, the least interorbital width being between one-third and a half of skull roof midline length; in *Blinasaurus* it is between a quarter and a half. The supraorbital canals of the lateral line system extend back onto the parietal and supratemporal bones and are not joined to the infraorbital and temporal canals on the postorbital bones as in *Blinasaurus*.

Boreosaurus. The adductor fossa of the lower jaw is comparatively smaller than in *Blinasaurus*: the greatest length of this fossa is about a quarter of lower jaw length from the symphysis to the anterior edge of the articular facet; in *Blinasaurus* it is between one-third and a half.

Hadrokkosaurus. The adductor fossa is comparatively smaller than in *Blinasaurus*: the greatest length of this fossa is about one-third of lower jaw length from the symphysis to the anterior edge of the adductor fossa; in *Blinasaurus* it is between one-third and a half. The

¹*Blina*—with reference to the station property on which the holotype skull was found plus *Saurus*—lizard.

²I accept responsibility for this status of the name as I furnished it in correspondence to Dr. A. S. Romer, anticipating the publication of this article prior to the publication of his text.

labial surface of the lower jaw is devoid of the sculpture present on *Blinasaurus* but contains a lateral mandibular fenestra absent on *Blinasaurus*.

Blinasaurus wilkinsoni (Stephens, 1887)

Platyceps wilkinsoni Stephens (1887, p. 1175, pl. XXII; 1888, p. 156); Watson (1919, p. 48); von Huene (1956, p. 99); Romer (1947, p. 235).

"*Platyceps*" *wilkinsoni* Watson (1956, p. 338, figs. 11 and 33E, pl. 39); Hills (1958, p. 97).

Holotype, (by monotypy), N.S.W.G.S. no. F12872, a partial skeleton, consisting of the skull roof, a number of branchial bars, the dermal shoulder girdle and a series of ribs and vertebral elements.

Type locality. The Railway Ballast Quarry near Gosford, New South Wales (Wilkinson in Woodward, 1890, p. V and David in Woodward, 1890, pp. VII-IX, pl. A). The stratigraphic column included in David's plate A shows the fish-bed as a 5 ft. 9 in. thick layer of purplish gray sandy shale and laminated mudstone. The upper surface of this layer lies 46 ft. below the top of the quarry.

Horizon. Uppermost part of the Gosford Formation, Narrabeen Group. Middle Triassic.

Diagnosis. The orbits are relatively smaller than those of *Blinasaurus henwoodi*; the orbital length as measured on the midline is only about a quarter of the midline length of the skull roof whereas in *B. henwoodi* it is nearly one-third. (The significance of this difference is increased by the fact that the holotype skull is much smaller than the holotype skull of *B. henwoodi* and small, immature labyrinthodonts usually have relatively larger orbits than larger individuals of the same species. The parietal and post-orbital bones are in sutural contact whereas in *B. henwoodi* they are separated by a sutural contact of the postfrontal and supratemporal bones. The frontal bone is separated from the medial margin of the orbit whereas in *B. henwoodi* the frontal bone forms part of the medial margin.

Remarks. A new illustration of the skull roof and dermal shoulder girdle (Fig. 3) is attempted which differs from Watson's (1956 fig. 11) in several respects. The preorbital region of the skull is reduced in relative size. The tabular bones appear to be larger and the postparietal bones smaller than shown by Watson. Portions of the lateral line system not shown by Watson are faintly indicated on the specimen. The supraorbital canals curve around the medial margins of the orbits, passing through the postfrontal and postorbital bones. The temporal canals are joined to the supraorbital canals in the postorbital bones and extend back through the supratemporal and tabular bones to the posterior edge of the skull roof.

As shown by Watson the parietal bone has a lateral border on the postorbital bone, an unusual condition which also occurs in *Dvinosaurus primus* (Bystrov 1938, fig. 6) and *Tupilakosaurus wetlugensis* (Shishkin, 1961, fig. 1). The frontals are excluded from the medial orbit margins by the postfrontals and prefrontals.

The sculpture pattern is the usual reticulate variety found in the Brachyopidae and, as shown by Watson (1956), The occipital structures are typical of the family. The descending process of the squamosal is concave in posterior view and the occipital processes of the postparietals and tabulars slope down and back from the skull roof.

The external impressions of the articulated interclavicle and clavicles lie just behind the skull. The sculpture preserved on these impressions, very fine and even in texture, consists mainly of closely spaced radiating ridges. Pitted sculpture was probably present at the ossification centres of the bone but preservation of the impressions is not good enough to be certain of this. The cleithral processes of the clavicles, located at the posterolateral corners of the bones, have a pronounced backward slope as is the case in other brachyopids. The interclavicle has a straight posterior border in contrast to most other labyrinthodonts where the posterior border of this bone is bluntly rounded.

Nineteen pairs of neural arch pedicles, each pair flanked by a pair of ribs, extend back from the posterior border of the interclavicle. The pedicles are the only parts of the vertebrae preserved. The neural spines must have been imbedded in the missing counterslab of the specimen. The central elements were apparently unossified as small excavations were made along the vertebral column and no bone could be found between, under or on either side of the pairs of arch pedicles. The ribs are narrow-waisted and have expanded proximal and distal ends. The proximal ends appear to be single headed.

*Blinasaurus henwoodi*¹ sp. nov.

Holotype. W.A.M. no. 62.1.42, a fairly complete skull.

Type locality. U.C.M.P. locality V6041, Erskine Range, on Blina Station, West Kimberley District, Western Australia. The specimen was found as float. The buff shale matrix indicates derivation from the Blina Shale rather than from the overlying Erskine Sandstone although it does not match the shale at the place where it was found. It is very close in color and texture to several shale lenses farther up the slope but it could not be matched exactly with any of them.

Horizon. Upper Blina Shale, ? Otoceratan Division of the Scythian Stage.

Diagnosis. The orbits are relatively larger than those of *B. wilkinsoni*—see the diagnosis of this species—the orbital length as measured on the midline being nearly one-third of the midline length of the skull whereas in *B. wilkinsoni* it is only about a quarter. The parietal bone is separated from the postorbital bone by a postfrontal-supratemporal suture whereas in *B. wilkinsoni* they are in sutural contact. The frontal bone forms part of the medial margin of the orbit whereas in *B. wilkinsoni* it is excluded from this margin by a prefrontal-postfrontal suture.

¹ The species is named for Mr. J. Henwood of Blina Station who permitted the excavation of the Erskine Range quarries which lie on the Blina property and who extended much hospitality to the field party.

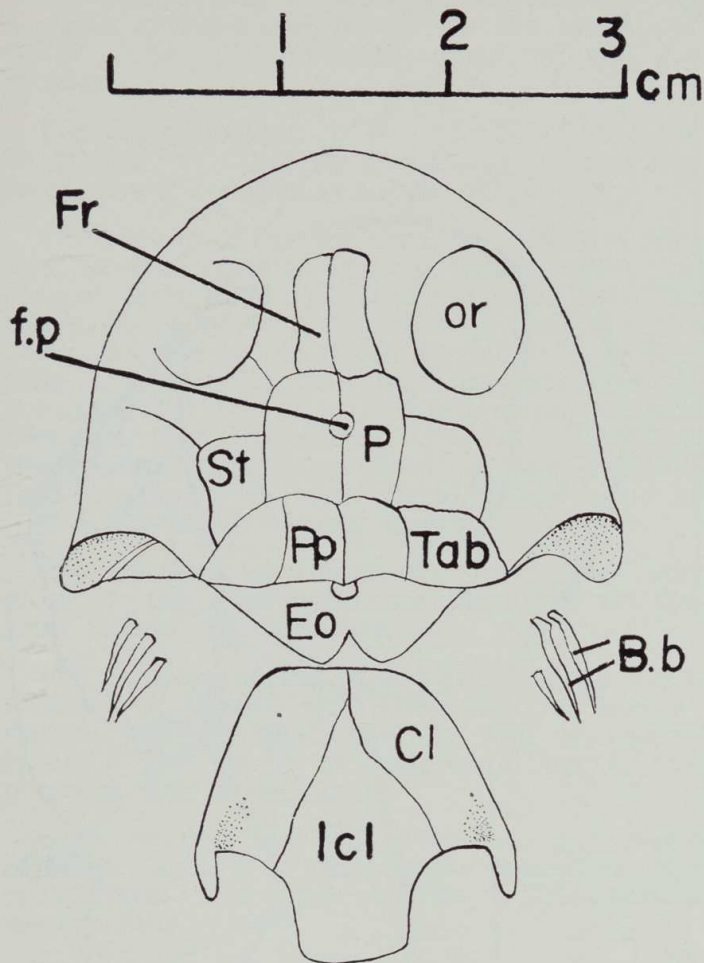


Figure 3.—*Blinasaurus wilkinsoni* (Stephens, 1887), holotype, NSWGS no. F12872; skull, dermal shoulder girdle and branchial bars, dorsal view.

Abbreviations for Figure 3 and following Figures: *Ang*, angular; *B.b*, branchial bars; *c.bo*, basioccipital space; *c.so*, supraoccipital space; *Cl*, clavicle; *Cor*, coronoid; *Den*, dentary; *Ecpt*, ectopterygoid; *Eo*, exoccipital; *f*, foramen, *f.m*, foramen magnum; *f.m.p*, posterior meckelian foramen; *f.p*, parietal foramen; *ja.a*, articular facet; *je.po*, pteroccipital fenestra; *fo.ad*, adductor fossa; *fo.pt*, post-temporal fossa; *fo.ra*, retroarticular fossa; *fo.st*, subtemporal fossa; *Fr*, frontal; *Icl*, interclavicle; *Ico*, intercoronoid; *ip.v*, interpterygoid vacuity; *Ju*, jugal; *La*, lacrimal; *Mx*, maxillary; *n.i*, internal naris (choana); *n.e*, external naris; *Na*, nasal; *or*, orbit; *P*, parietal; *p.c*, cultriform process; *p.po*, paraoccipital process; *p.poc*, postcondylar process; *p.quj*, descending process of the quadratojugal; *p.ra*, retroarticular process; *p.sq*, descending process of the squamosal; *p.v*, vertical process; *Pa*, prearticular; *Pco*, precoronoid; *Pf*, postfrontal; *Pl*, palatine; *Pm*, premaxillary; *Po*, postorbital; *Pos*, postsphenial; *Pp*, postparietal; *Prf*, prefrontal; *Ps*, parasphenoid; *Pt*, pterygoid; *Qu*, quadrate; *Quj*, quadratojugal; *s.io*, infraorbital groove; *s.j*, jugal groove; *s.so*, supraorbital groove; *s.t.*, temporal groove; *Sa*, surangular; *Smx*, septomaxillary; *Sp*, splenial; *Sq*, squamosal; *St*, supratemporal; *sym*, symphysis; *t*, tusk; *Tab*, tabular; *Vo*, vomer.

Paratypes. Articulated lower jaws, W.A.M. no. 63.8.26 from U.C.M.P. locality V6040 and U.C.M.P. no. 61065 from V6043. Incomplete lower jaws W.A.M. nos. 60.9.15, 63.8.261, 64.7.15, 64.7.16, 68.5.61 and 68.5.62, U.C.M.P. nos. 61066, 61069, 61070, 61075 and 61076; all from U.C.M.P. locality V6040. Incomplete lower jaw, U.C.M.P. no. 61142 from U.C.M.P. locality V6046. Partial clavicles, U.C.M.P. nos. 61078, 61086, and 61093 from U.C.M.P. locality V6040.

Description. *Skull roof* (Figs. 4a and 6a). The outer portions of the holotype skull are broken and weathered. Most of the bone is missing from the dorsal surface but the internal mould preserves sutures, traces of the sensory canals and even of the grain of the bone. Small areas of bone between the orbits and nares and on the right postorbital preserve the external ornament.

The dorsal surface of the skull, as reconstructed in Figure 6a, is shield shaped. The lateral borders were reconstructed by projecting the sloping lateral portions of the skull roof down to the level of the palate. The curvatures of these borders were then projected around the orbits to converge at the snout tip.

The occipital border of the skull projects backwards at the midline and at rudimentary tabular horns. Between these projections and between the tabular horns and the posterolateral skull corners the occipital edge is concave.

The interorbital portion of the skull roof is shallowly concave about the midline. A swollen area occurs behind of each orbit. The skull table slopes down and back from these elevations to the posterior corners of the skull.

Viewed in profile (Figs. 4b and 6b), the skull is very shallow in the orbital and preorbital regions. The cheek becomes deep behind the orbit and attains a considerable depth just anterior to the quadrate condyles.

The nearly complete left external naris is large and has a raised rim. It is almost shaped with the long axis set at about 45° to the midline of the skull.

The premaxillary, maxillary, jugal and quadratojugal bones of the reconstruction are based on analogy with *Batrachosuchus watsoni*.

The small nasals form the posteromedial borders of the external nares. Nasal-lacrimal and nasal-premaxillary sutures are not preserved but the lateral border of the left nasal on the prefrontal can be seen with the aid of a ten-power microscope. The actual course of the nasal frontal sutures could not be found but remnants of the pattern of surface sculpture in this area limit the location of these sutures to a position anterior to the orbits.

The conjoined frontals are cruciform in shape. Each frontal is indented anteriorly by the prefrontal and posteriorly by the post-frontal and has a short border on the orbit.

The large parietals occupy the centre of the postorbital part of the skull roof. The parietal foramen, 6 mm in diameter, is located on the midline about 3/5 of the length of the parietal back from its forward edge. Impression of bone grain shows that the centre of ossification of each parietal lay close to the lateral edge of the parietal foramen.

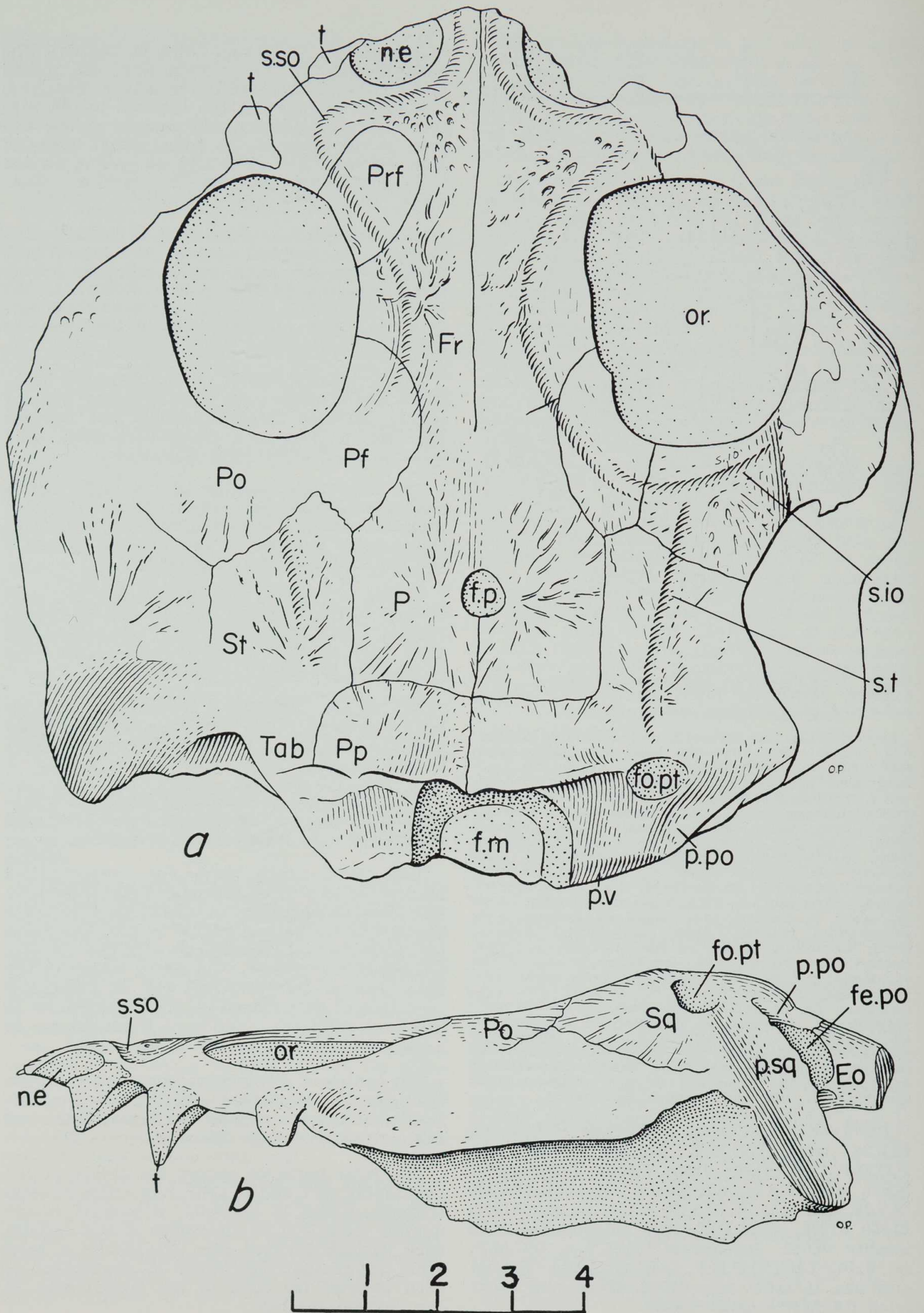


Figure 4.—*Blinasaurus henwoodi* sp. nov., holotype. W.A.M. no. 62.142; skull: a, dorsal view; b, lateral view.

The postparietal is nearly rectangular and has a short anterolateral border on the supratemporal. The posterolateral edge adjoins the tabular.

The entire margin of the left prefrontal can be traced. The bone is small and circular and forms the anteromedial border of the orbit.

The portion of the skull roof between the orbit and external naris is entirely hypothetical. The reconstructed skull outline leaves ample room for the inclusion of both the lacrimal bone and the dorsal process of the maxillary bone. It is possible, however, that this bone was absent from the skull roof as it is in *Batrachosuchus watsoni* (Watson, 1956, Fig. 5). It is also possible that the septomaxillary, posterior to the external naris in Figure 6a, was lateral to the naris as it is in the South African species.

The outlines of the entire postfrontal and most of the postorbital are preserved on the right side of the skull roof.

The outlines of the supratemporal are more complete on the left side. Anteriorly it is narrow, making only a small contact with the postfrontal. The centre of ossification lay in the posterior half of the bone.

Both tabulars are badly eroded. As reconstructed, each is a small bone lateral to the postparietal and each carries a rudimentary tabular horn.

The left squamosal occupies the central part of the downwardly sloping skull corner. Anteriorly it is bordered by the squamosal-postorbital and squamosal-supratemporal sutures.

Sculpture is preserved on the nasals, the left frontal and the right postorbital. The latter displays the sculpture pattern most commonly found in Triassic labyrinthodonts, namely a central faveolate area surrounded by radiating grooves and ridges. The nasals have only pits. The anterior part of the left frontal has longitudinal grooves and ridges.

The supraorbital canals are well-defined on frontal, prefrontal and nasal bones in the central region between the orbits and external nares. They are 2 to 3 mm wide and 1 mm deep. The right one is faintly indicated on an internal mould surface behind the orbit. The canals are divided by a sharp ridge at the median sutures of the premaxillaries and nasals. Behind this ridge each canal diverges laterally to follow the posterior border of the external naris and makes a very tight loop anterior to the orbit (perhaps within the lacrimal bone). The right supraorbital canal parallels the medial border of the orbit, crossing the prefrontal, frontal and post frontal bones, and joins with the intra-orbital and temporal canals in the centre of the postorbital bone.

The right temporal canal runs posteromedially through the postorbital and supratemporal bones. The surface of the tabular is battered and it is uncertain if the temporal canal extended into it.

A short portion of the right infraorbital canal is preserved on the mould surface of the right postorbital bone. The remainder of this canal and the jugal canal, as shown in Figure 4a, is taken from *Batrachosuchus watsoni* (Watson, 1956, Fig. 6a.)

Palatal surface (Figs. 5a and 7a). This surface was encased in a layer of matrix. Hollow moulds of large palatal tusks, exposed on the edges of the specimen, were filled in with dental plaster. Preparation of the palate revealed a surface partly composed of bone and partly of internal cast. Several lumps of hard hematite obscured bone relations in the anterior part of the palate.

Very large, triangular interpterygoid vacuities occupy most of the palate surface. The medial margin of each is longer than the lateral margin and its lateral corner lies opposite the anterior edge of the subtemporal fossa.

Each subtemporal fossa, as restored, is very long and narrow. It reaches from the posterolateral corner of the palate to the level of the lateral corner of the interpterygoid vacuity. Each fossa is medially bounded by the pterygoid. The jugal and quadratojugal undoubtedly formed the lateral border in the original complete skull and an alar process of the jugal may have formed the anterior border of each fossa.

The parasphenoid consists of a large subquadrangular plate beneath the braincase and a narrow cultriform process which extends forward separating the posterior projections of the vomers. The cultriform process has a narrow waist in the middle of its length.

A small scrap of exoccipital remains on each posterolateral corner of the basal plate, separated by a suture from the parasphenoid and pterygoid.

The lateral parts of the pterygoid bones bend sharply downward in characteristic brachyopid fashion, giving a very concave shape to the posterior part of the palate. Each pterygoid extends forward at least as far as the anterior edge of the subtemporal fossa.

Three tusks are preserved on the anterolateral margin of the left interpterygoid vacuity and two along the right interpterygoid vacuity. The tusks are conical and vertically striated. The middle tusk of the left side is complete to the tip which points slightly inward. The posterior tusk of the left side is smaller than the others. The spacing of these tusks indicates that each is a member of a pair and that each was originally flanked by a replacement pit. It seems certain that the anterior tusks are located in the vomers, the central tusks in the palatines and the posterior tusk in the ectopterygoid. The spacing of the tusks indicates that the vomers were large as in *Batrachosuchus watsoni* and that the palatines and ectopterygoids were small. The sutures of the restoration are based on *B. watsoni*.

A small round choana is located slightly internal to the two anterior tusks of the left side. Its outer margin may be traced for a short distance but the remainder is obscured.

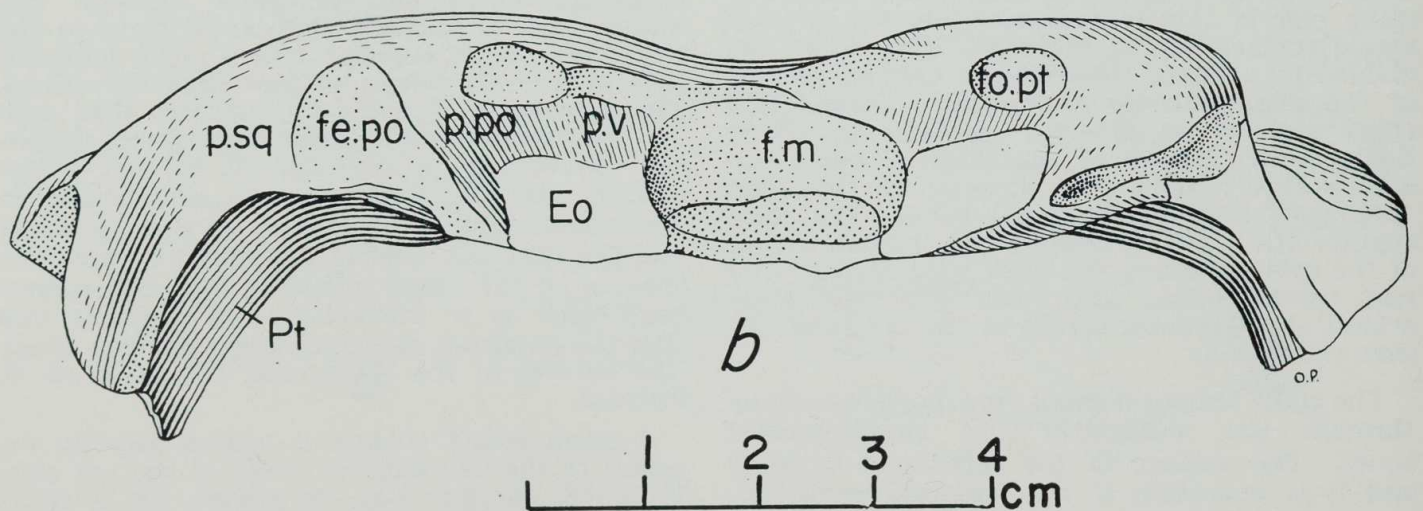
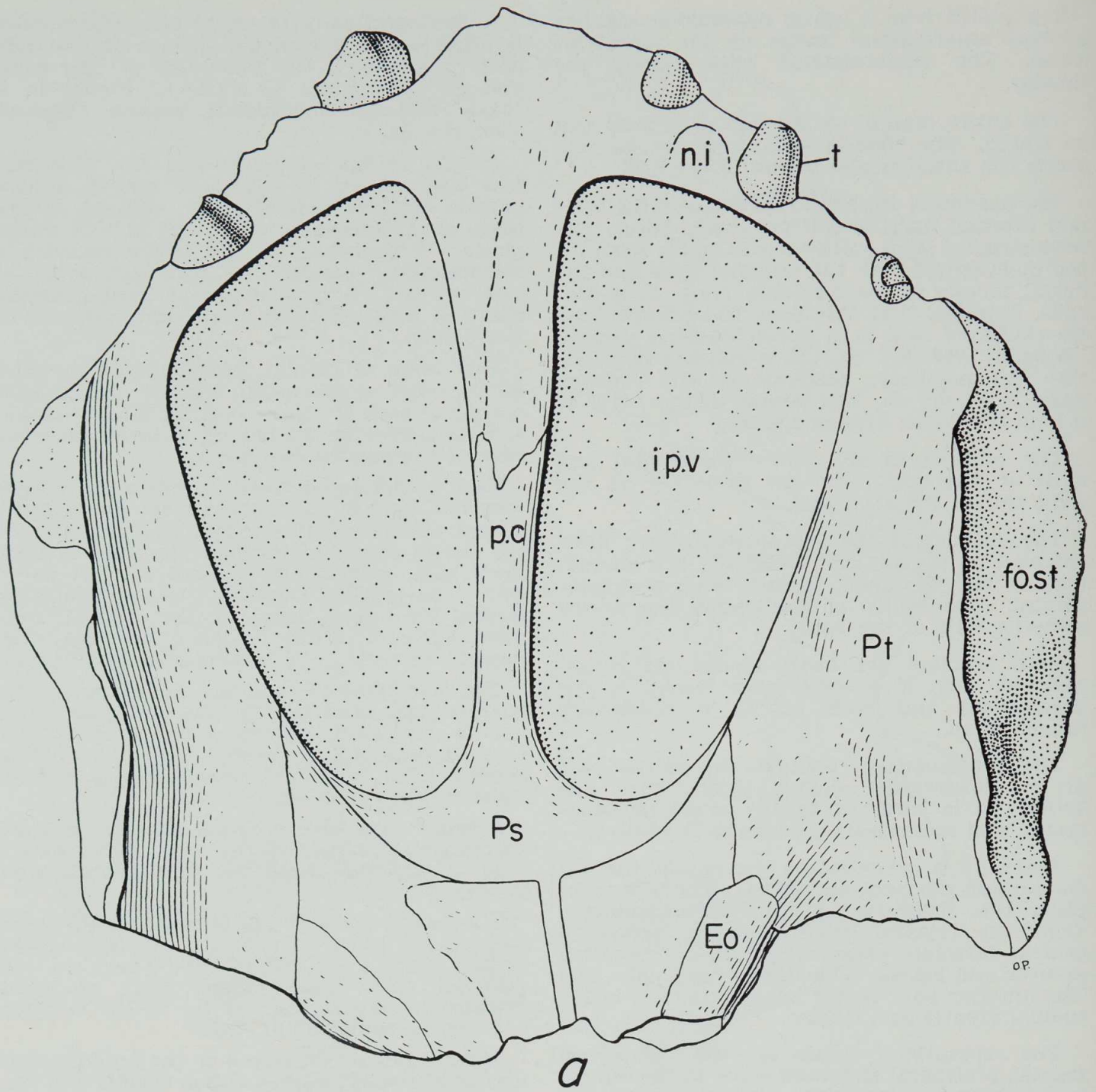


Figure 5.—*Blinasaurus henwoodi*, sp. nov., holotype, W. A.M. no. 62.1.42; skull; a palatal view; b, occipital view.

Occipital surface (Figs. 5b and 7b). The occipital and quadrate condyles are missing but portions remain of the dorsomedial and lateral regions.

The outlines of the occiput are characteristically brachyopid as the lateral portions bend sharply downward as in *Bothriceps australis* (Watson, 1956, Fig. 1b.) and *Batrachosuchus watsoni* (ibid., Fig. 5b). The central region of the palate, formed by the parasphenoid plate, is slightly convex downward as in the above genera. The rear border of the skull table, which is straight in *Bothriceps* and *Batrachosuchus*, is concave upward about the midline in the Australian brachyopid.

The foramen magnum is flanked by broad bony structures which have been pushed down and backward by dorsoventral compression of the skull. Each structure is bifurcated near its centre, the medial branch being the vertical column and the lateral branch the paraoccipital bar. Lamellosus and basalis processes, which delimit the spaces for the cartilaginous supraoccipital and basioccipital bones from the foramen magnum in other brachyopids, are not preserved on the medial surfaces of the vertical columns of the *Blinasaurus henwoodi* skull. No sutures separating the exoccipital bone below from the tabular and postparietals bones above are preserved on the structures. The structure of the left side retains the broken neck of the exoccipital condyle which is round and suggests that the condyle was high and rounded as in other brachyopids.

The descending process of the squamosal, preserved on the left side of the occiput, is concave posteriorly about a vertical axis as in all brachyopids. The ventral parts of this descending process may actually be the quadratojugal but no suture was found. A narrow gap of matrix, originally occupied by palatoquadrate cartilage, separates it from the posterior edge of the descending wing of the pterygoid. The posterior edges of both the descending process of the squamosal and the pterygoid are chipped and eroded.

An open space, the pteroccipital fenestra, lies above the horizontal part of the pterygoid between the squamosal and the paraoccipital bar. It accommodated the passage of the stapes to the side wall of the otic capsule. The stapes is not preserved.

Measurements.

Skull roof

Length from the midline rear of the skull roof to the posterior edge of the parietal foramen	2.4 cm.
Length from the midline rear of the skull roof to the level of the posterior edges of the orbits	4.7 cm.
Length from the midline rear of the skull roof to the anterior edges of the orbits	8.2 c.m.
Length from the midline rear of the skull roof to the level of the posterior edges of the external nares	9.5 cm.

Anteroposterior length of the left orbit	3.5 cm.
Greatest width normal to the length of the left orbit	2.7 cm.
Least interorbital width	3.1 cm.
Greatest diameter of the left external naris	1.4 cm.
Diameter of the parietal foramen	0.6 cm.
Palatal surface	
Anteroposterior length of the right interpterygoid vacuity	7.0 cm.
Greatest width normal to the length of the right interpterygoid vacuity	3.3 cm.

Lower jaw (Figs. 8-10). A pair of fused lower jaws, U.C.M.P. No. 61065 (Figs. 8c-f), from the quarry at V6043, closely matches the parabolic skull outline of *Blinasaurus henwoodi*. The specimen was found dorsal side up on the ripple-marked surface at V6043. The right side is the better preserved and retains its natural shape. The outlines of the articular facet and the adductor fossa are nearly complete. The dentition, with the exception of a badly preserved symphyseal tusk, is missing. Leached bone constitutes the retroarticular process and the articular facet and covers the labial side. The lingual side is mainly internal cast with a few scraps of bone. The size and shape of the reconstructed internal cast (Fig. 9) are based on this specimen and the sutures shown are adapted from the fragmentary specimens, U.C.M.P. Nos. 61069 (Fig. 10) and 61142 (Figs. 8a and 8b).

The jaw is bowed upward in the lingual and labial views to match the concavity of the palate. The symphyseal region is very narrow and is rounded in section. (Part of the thickness of the symphyseal region shown in the reconstructions is probably composed of the deeper layers of dermal bone surrounding the internal mould. Bone and mould could not be distinguished in this region of no. 61065.) The area between the symphyseal region and the adductor fossa is high and narrow, is inclined ventromedially and has a keeled ventral surface. The jaw widens in dorsal view through the region of the adductor fossa and the articular facet. A flat ventral surface underlies the anterior half of the adductor fossa. The ventral surface from the centre of the adductor fossa to the tip of the retroarticular process is keeled.

The large adductor fossa is triangular in dorsal view with a flat posterior margin and an acute anterior margin. The labial wall is very high and has a rounded upper margin. The lingual wall is low and its upper margin is concave downward.

The articular facet is sharply defined by high pre- and post-condylar processes and is crossed by a low diagonal swell which runs from the outer corner of the postcondylar process to the inner corner of the precondylar process. Lingually, the articular facet is produced into a ledge which overhangs the surface of the jaw below it.

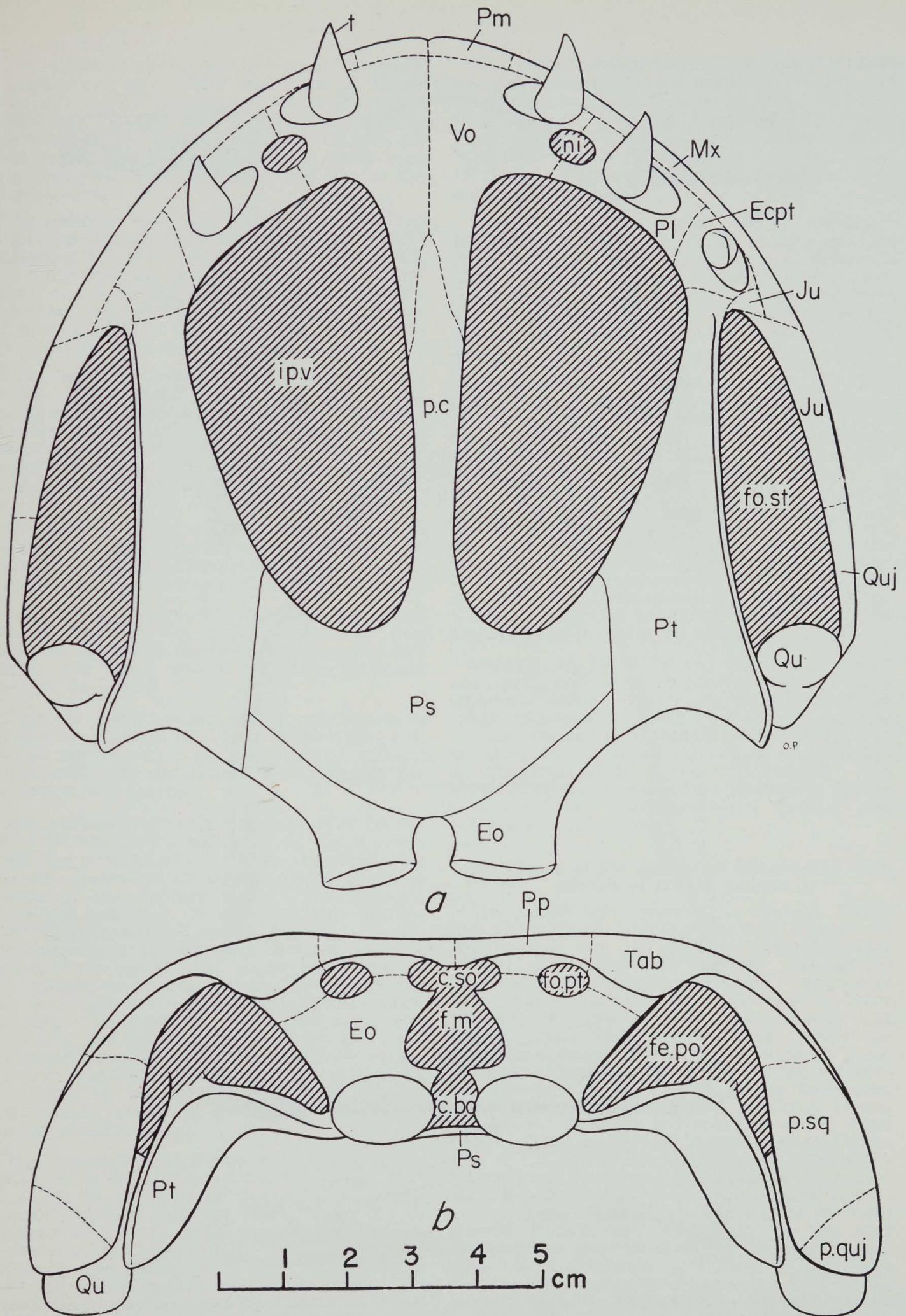


Figure 7.—*Blinasaurus henwoodi* sp. nov., reconstruction of the skull based on W.A.M. no. 62.1.42: a, palatal view; b, occipital view.

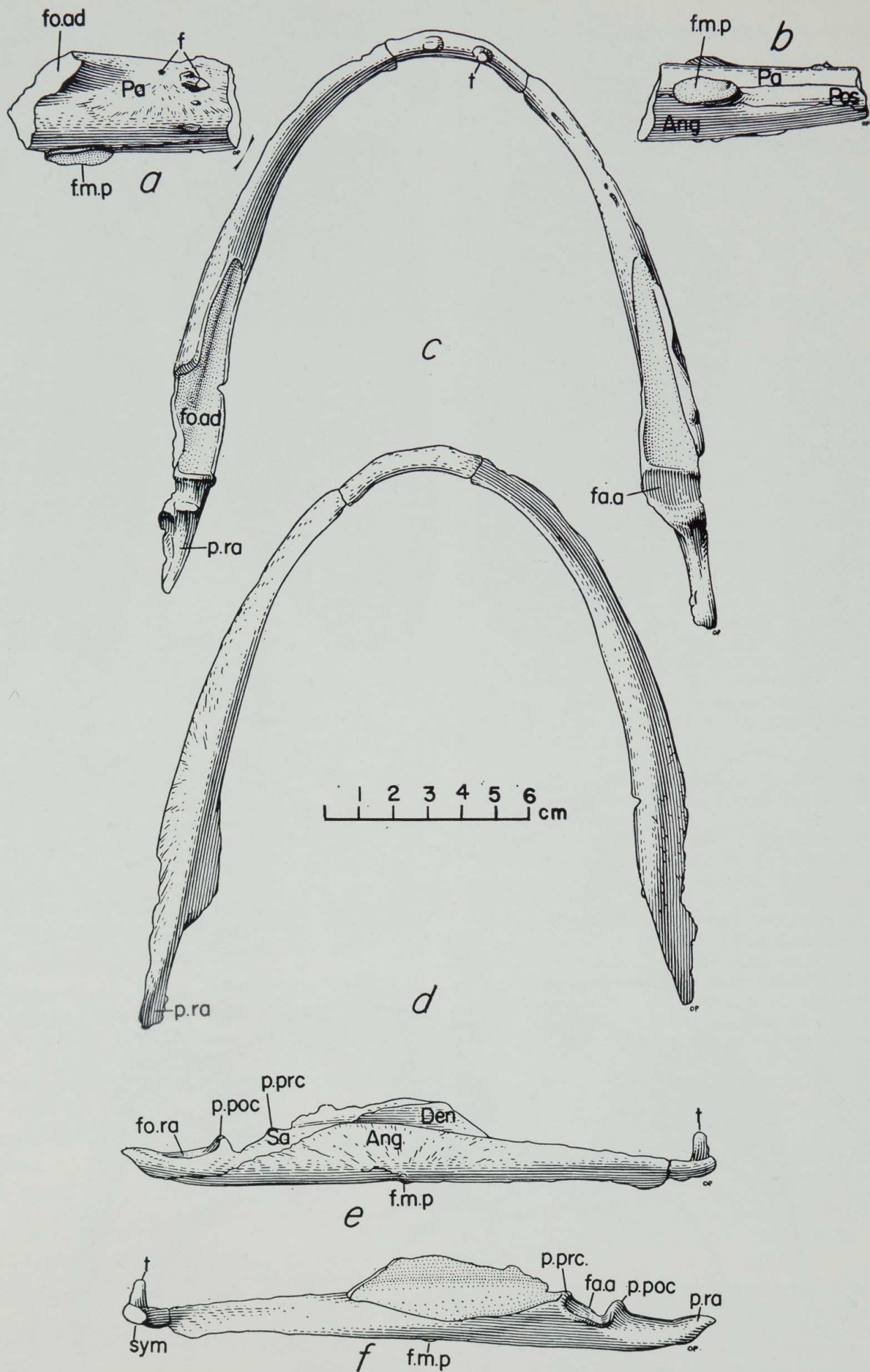


Figure 8.—*Blinasaurus henwoodi*, sp. nov., paratypes; a, U.C.M.P. no. 61142, lower jaw fragment, lingual view; b, the same, ventral view; c, U.C.M.P. no. 61065, lower jaw, dorsal view; d, the same, ventral view; e, the same labial view; f, the same, lingual view.

The narrow retroarticular process is triangular in section and has a long groove on its dorso-labial side for the insertion of the *m. depressor mandibulae*. Bits of bone broken from the surface of the retroarticular process of U.C.M.P. no. 61069 reveal a matrix-filled interior which may have contained a cartilaginous extension of the articular bone.

The posterior meckelian foramen is preserved as an oval protuberant infilling on the ventral surfaces of U.C.M.P. nos. 61069, 61142 and 61065. It is 6 mm long on the first, 20 mm long on the second and 5 mm long on the last. It is directly under the anterior edge of the adductor fossa of U.C.M.P. no. 61142 but somewhat posterior to this point in the other two specimens.

The dentary impression covers a large area on the labial surface and a small area on the lingual surface of U.C.M.P. no. 61069. It extends onto the labial wall of the adductor fossa as a slender and pointed process. The internal surface of this process is retained as a groove on the surangular bone of the right half of U.C.M.P. no. 61065.

The borders of the coronoid bone are clearly marked on the internal mould surface of U.C.M.P. no. 61069. The bone is oval and forms the entire anterior edge of the adductor fossa.

The impression of the intercoronoid bone, best seen on U.C.M.P. no. 61069, is anterior and somewhat ventral to the coronoid. It is oval and has a low swell which runs longitudinally through its centre.

Only the posterior part of the precoronoid is retained on U.C.M.P. no. 61060. This is long and narrow and carries a small cylindrical infilling which marks the site of a foramen, possibly the postsymphysial foramen.

The angular bone covers a large area on the labial surface of the right half of U.C.M.P. no. 61065 and is dorsally bordered by the surangular and the groove which contained the posterior process of the dentary bone. The remnants of dermal sculpture retained on this surface show that broad ridges and grooves of the standard labyrinthodont pattern radiate out from the centre of the lower edge. A lingual process of the angular is lacking as in *Batrachosuchus* and the course of the angular-prearticular internal suture, traceable on the ventral surface of no. 61069, runs longitudinally from the tip of the retroarticular process to the rear border of the posterior meckelian fenestra. The pattern of bone grain on U.C.M.P. no. 61069 indicates the approximate position of the anterior part of the angular-dentary suture.

The surangular, preserved as actual bone on both sides of U.C.M.P. no. 61065 and on U.C.M.P. no. 61069, forms the upper portions of the retroarticular process and the labial walls of the adductor fossa. The dorsal surface on the retroarticular process contains the fossae for the *m. depressor mandibulae*. The anterior portion of the labial wall of the adductor fossae on the right half of U.C.M.P. no. 61065 contains the groove for the dentary process.

The prearticular of U.C.M.P. no. 61069 consists of actual bone on the retroarticular process and of internal impression on its more anterior portions. It forms the lower margin of the articular facet and the lingual wall of the adductor fossa (although this is broken away on the present specimen). Anteriorly, it is bordered by the coronoid and precoronoid.

Dermal shoulder girdle. Three clavicular fragments, U.C.M.P. nos. 61078, 61086 and 61093 (Fig. 11), are referred to *Blinasaurus henwoodi* on the basis of external sculpture and conjectured position of the cleithral process. All three are external moulds of the ventral plate of the clavicle and all were found on the surface at V6040.

The sculpture pattern is quite distinct from that found on several dermal shoulder elements of *Deltasaurus kimberleyensis* found at V6040. Large coarse ridges, some of which anastomose and bifurcate distally, radiate from the ossification centres at the posterolateral corners. A finer vermiculose pattern of small pits, ridges and nodes covers the sides of the large ridges and the surfaces of the grooves between them. The large ridges resemble those found on the clavicles of *Hadrokkosaurus bradyi* (Welles, 1947, Fig. 8) and on four clavicular fragments of unpublished *Batrachosuchus* material in the U.C.M.P. collection but these genera lack the finer pattern between the ridges.

U.C.M.P. No. 61086, shows small portions of the lateral and posterior borders near the posterolateral corner. The angle formed by these ridges indicates that the base of the cleithral process was more posteriorly placed relative to the posterior border of the ventral plate of the clavicle than it is in the rhytidosteid. The cleithral process has a similar position in *Batrachosuchus* sp., *Hadrokkosaurus bradyi* and *Blinasaurus wilkinsoni*.

Comparisons of the species of *Blinasaurus* with species of related genera

The family was reviewed by Watson (1956) and much of the information that appears in this section for the species *Batrachosuchus browni*, *Batrachosuchus watsoni*, *Blinasaurus wilkinsoni*, *Bothriceps australis*, *Brachyops laticeps* and *Trucheosaurus major* is taken from this excellent report. The measurements and indices listed for *Batrachosuchus browni* on Table 1 are based on Figure 8 of Watson's work. The measurements and indices for the remaining species are taken from actual specimens, most of which are holotypes and only known specimens. Through the courtesy of Dr. Alan Charig, Curator of Fossil Amphibians and Reptiles at the British Museum (Natural History) I was able to study the holotypes of *Batrachosuchus watsoni*, *Bothriceps australis* and *Brachyops laticeps*. Through the courtesy of Dr. John Pickett, Curator of Paleontology at the New South Wales Geological Survey, the holotype of *Blinasaurus wilkinsoni* and part of the holotype of *Trucheosaurus major* were lent to me while I was at the University of Tasmania. This allowed direct comparisons of these specimens

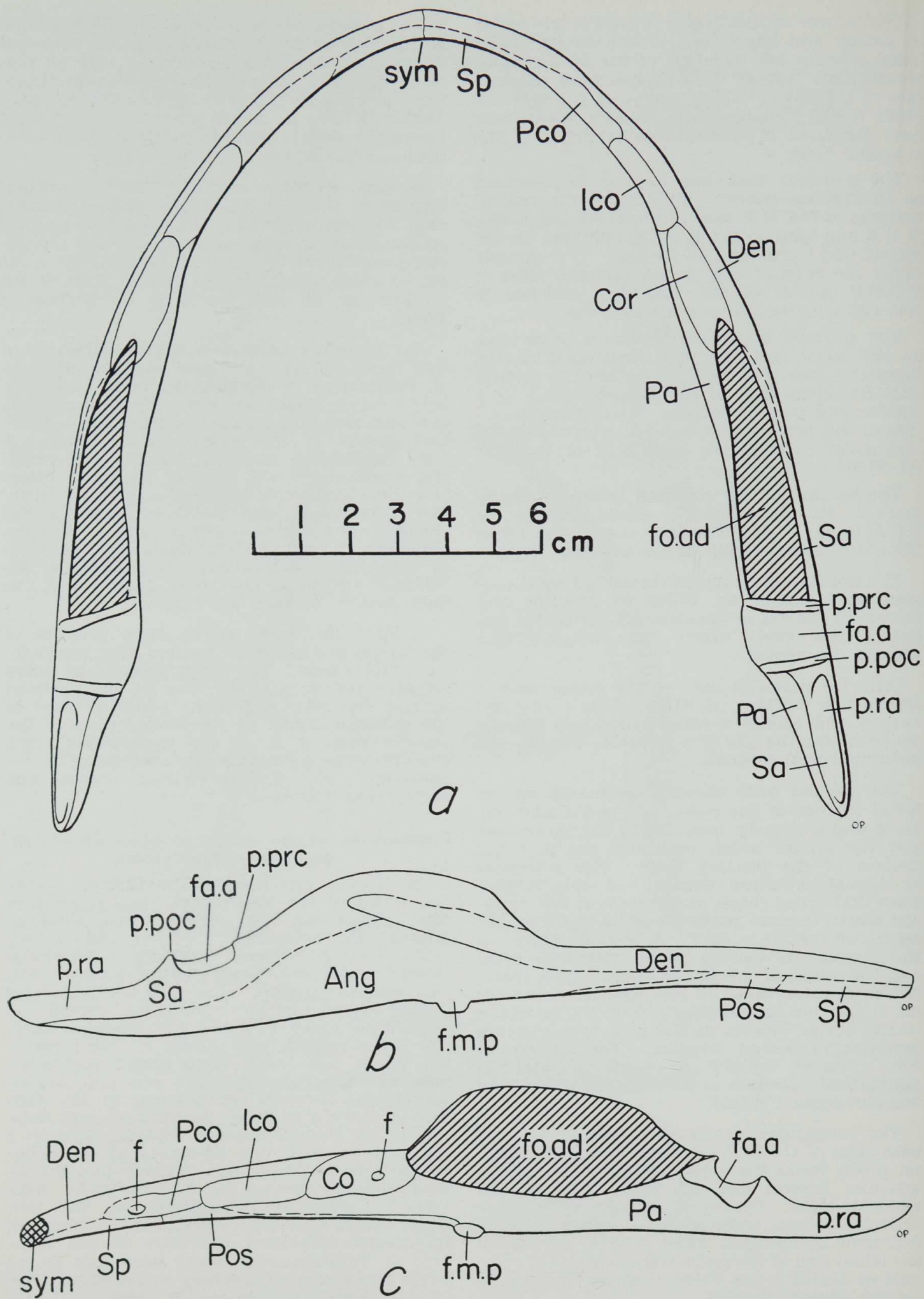


Figure 9.—*Blinasaurus henwoodi*, sp. nov., reconstruction of the internal surfaces of the bones of the lower jaw, based on U.C.M.P. nos. 61065, 61069 and 61142: a, dorsal view; b, labial view; c, lingual view.

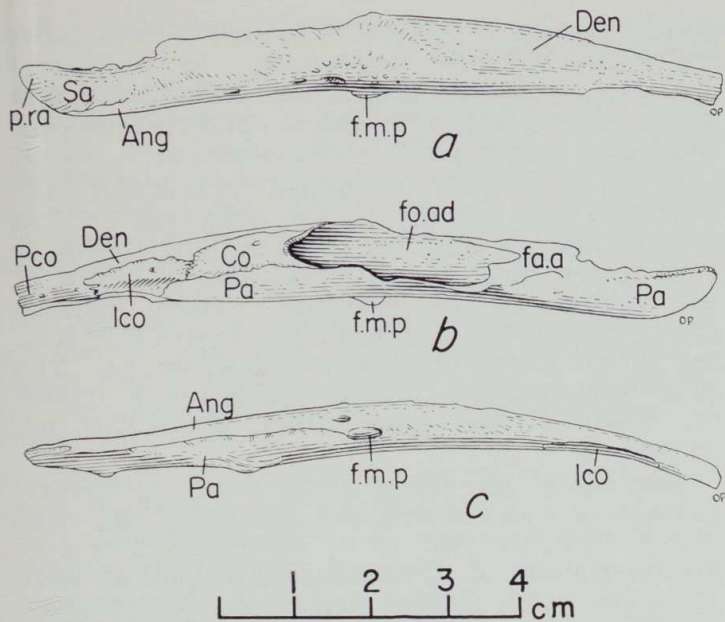


Figure 10.—*Blinasaurus henwoodi*, sp. nov., paratype, U.C.M.P. no. 61069, lower jaw: a, labial view; b, lingual view; c, ventral view.

with a plaster replica of the holotype of *Blinasaurus henwoodi* and with abundant cranial material of the Tasmanian *Blinasaurus*.

Comparisons with two brachyopids not considered in Watson's paper are also included in

this section. Information, measurements and indices for *Boreosaurus thorslundii* are taken from the text and figures of Nilsson (1943) and for the holotype lower jaw of *Hadrokkosaurus bradyi* from the text and figure of Welles (1947).

The comparisons of these species with the species of *Blinasaurus* are arranged below in an order that roughly corresponds with their stratigraphic order, beginning with the oldest species and ending with the youngest.

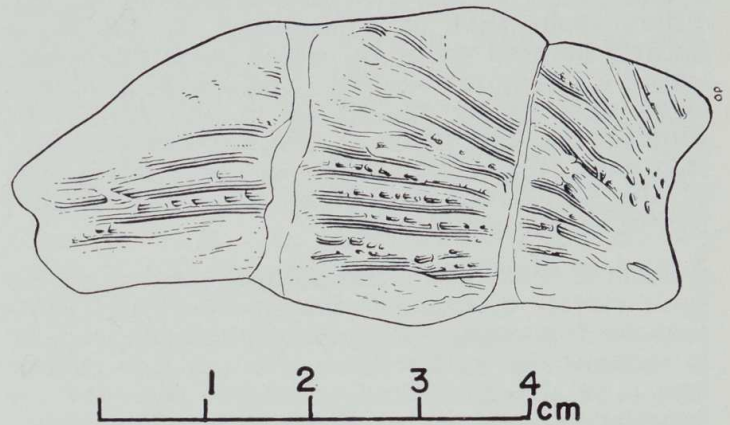


Figure 11.—*Blinasaurus henwoodi*, sp. nov., paratype, U.C.M.P. no. 61093, right clavicle; ventral view.

TABLE 1

Measurements and Indices	<i>Blinasaurus wilkinsoni</i> NSWGS F12872	<i>Blinasaurus henwoodi</i> WAM 62.1.42	<i>Bothriceps australis</i> BMNH 23110	<i>Trucho-saurus major</i> NSWGS F12697 Watson 1956	<i>Brachyops laticeps</i> BMNH R4414	<i>Boreosaurus thorslundii</i> Nilsson 1943 figs 21-24	<i>Batrachosuchus watsoni</i> BMNH R3489	<i>Batrachosuchus browni</i> Watson 1956 fig 8	<i>Hadrokkosaurus bradyi</i> UCMP 36199
Sagittal length of skull roof (A)	25 mm	111 mm	81 mm	50 mm	87 mm		155 mm	72 mm	
Length of orbits as measured on the midline (B)	6 mm	34 mm	22 mm	10 mm	20 mm		35 mm	15 mm	
Preorbital length of skull as measured on the midline (C)	6 mm	27 mm	27 mm	17 mm	24 mm		31 mm	16 mm	
Least distance between the orbits (D)	9 mm	31 mm	20 mm	23 mm	38 mm		71 mm	32 mm	
Greatest length of interpterygoid vacuities as measured on the midline (E)		70 mm	45 mm				80 mm		
Length of lower jaw from symphysis to articular facet outside curvature (F)		160 mm				102 mm			305 mm
Length of adductor fossa (G)		65 mm				25 mm			100 mm
B/A	0.24	0.31	0.27	0.20	0.23		0.23	0.20	
C/A	0.24	0.24	0.33	0.34	0.28		0.20	0.22	
D/A	0.36	0.28	0.25	0.46	0.44		0.46	0.45	
E/A		0.63	0.56				0.52		
G/F		0.41				0.25			0.33

Bothriceps australis Huxley, 1859. The original account of *B. australis* by Huxley (1859, p. 642, pl. 2, Figs. 1 and 2) was supplemented with further description and illustration by Broom (1915, p. 364, Fig. 2) and Watson (1919, p. 43, Fig. 20; 1956, p. 323, Figs. 1 and 2). The holotype and only specimen consists of a skull and attached, incomplete lower jaw, B.M.N.H. 23110. The origin of this specimen is not known with certainty but it is believed to come from a locality in the Upper Permian Lithgow Coal Measures of the Sydney Basin in New South Wales.

The skull, 81 mm in dorsal midline length, differs from that of *Blinasaurus* in having a slightly pointed snout tip which gives the dorsal aspect a triangular outline. The orbits, although large and closely spaced as in the species of *Blinasaurus* (see Table 1), are set relatively farther back on the skull roof; the preorbital length of the skull roof is 0.33 of the total midline length of the skull roof.

Several features of the palatal surface of the skull clearly distinguish this species from *Blinasaurus henwoodi*. Each interpterygoid vacuity is semicircular rather than triangular in outline and is relatively somewhat smaller than the interpterygoid vacuity of *Blinasaurus*. The vomer and palatine tusks are relatively smaller. The exoccipital-pterygoid sutures are very short. The broad subtemporal fossa is indented on its medial margin by a projection of the pterygoid bone, a feature observed in most labyrinthodonts but lacking in the Triassic brachyopids.

The lower jaw is more massive and less specialized than that of *B. henwoodi*. It lacks the distinct upward flexure observed on the lateral view of the lower jaw of the Western Australian species. The articular-prearticular suture and the posterior meckelian foramen lie low on the lingual surface rather than on the ventral surface.

Trucheosaurus major (Woodward, 1909). This species, based on a single specimen, was described and illustrated by Woodward (1909, p. 319, pl. LI) as *Bothriceps major*. The specimen consists of a skull and associated partial skeleton exposed in transverse section on a break surface through a matrix block. It is greatly compressed and poorly preserved. The containing block comes from the Upper Permian Lithgow Coal Measures and was found at the Commonwealth Oil Corporation Shale Mine at Airly, New South Wales. Its provenance is thus believed to be homotaxial with that of *Bothriceps australis*.

The specimen was divided after its discovery, part remaining at the Mining Museum of the New South Wales Geological Survey and part sent to the British Museum (Natural History). The portion at the Mining Museum contains the dorsal impression of the skull roof, the part described by Woodward (1909). Watson (1919, p. 43) commented on the portion at the British Museum (Natural History), B.M.N.H. no R3728. This consists of two blocks, one containing the ventral impression of the skull roof and the

other exposing 28 vertebrae with articulated ribs and also a few limb bones.

Watson (1956, p. 328, fig. 3) redescribed and reillustrated B.M.N.H. R3728 and placed the species in a new genus, *Trucheosaurus*.

I have recently examined N.S.W.G.S. no. F12697. Very few details are preserved on this portion but the outlines of the orbits, the margins of the skull and the positions of a few of the sutures can be discerned. These features closely match the corresponding ones of B.M.N.H. no. R3728 shown by Watson (1956, fig. 3). The measurements and indices given for *T. major* on Table 1 are taken from N.S.W.G.S. no. F12697.

The tip of the snout of *T. major* is slightly pointed and the triangular outline of the skull closely matches that of *B. australis*. The preorbital portion of the skull roof is long as in *B. australis*, being 0.34 of total skull roof midline length. The orbits, however, are relatively smaller and more widely spaced than in *B. australis* or in the species of *Blinasaurus*. The orbit length, as measured on the midline is 0.20 of total skull midline length and the least interorbital width is 0.46 of this measurement.

Brachyops laticeps Owen 1854. The holotype and only specimen, B.M.N.H. no. R4414, is an isolated skull from the Lower Triassic Mangali Beds near Nagpur, Central India. Until recently only the dorsal and occipital surfaces of the skull were exposed, the palatal surface remaining encased in matrix. The original account of these surfaces by Owen (1854, p. 473) was supplemented with further description and illustration by Broom (1915, p. 363, fig. 1) and Watson (1919, p. 44 and 1956, p. 330, figs. 4, 32D and 34C).

Dr. R. D. Estes of Boston University who is currently working on a review of the Brachyopidae in conjunction with Dr. S. P. Welles of the University of California recently corresponded with the authorities of the British Museum (Natural History) regarding the possibility of removing the matrix from the palatal surface of the skull. At his request the palatal surface was prepared by Mr. Rixon, preparator at the museum, and an account of the structure of this surface will be included in a forthcoming review by Welles and Estes.

Brachyops laticeps is intermediate in two respects between *Bothriceps australis* and the species of *Blinasaurus*. The snout region, viewed from above, is more pointed than in the *Blinasaurus* species but not to the degree observed in *Bothriceps australis*. The relative length of the preorbital portion of the skull is greater than that found in *Blinasaurus* but less than that found in *Bothriceps australis*; the preorbital length, measured on the midline, is 0.28 of total midline length of the skull roof. The orbits are set far apart and, in this respect, *Brachyops laticeps* resembles *Trucheosaurus major*; the least interorbital width is 0.44 of the total midline length of the skull roof.

Boreosaurus thorslundi Nilsson, 1943. The material included in this taxon by Nilsson (1943, p. 34, Figs. 21-35, pl. 9) consists entirely of

lower jaw fragments from the Sticky Keep Formation of Spitsbergen. These fragments were originally included in the hypodigm of *Aphaneramma* sp. 2 by Säve-Söderbergh (1936, pl. 21, Figs. 7-9). The holotype of the new species selected by Nilsson (1943, Figs. 21-24, pl. 9) is P.I.U. No. U.45, "an almost complete natural cast of the meckelian space (with the articular) of the left side," found at Mt. Milne Edwards. Paratypes include P.I.U. No. U.61 (op. cit., Fig. 25), "a fragment of the posterior part of the left ramus of a lower jaw" from Sticky Keep and S.M.N.H. No. ENS 337, a fragment of the posterior part of the right ramus of a lower jaw from Mt. Congress.

Nilsson reconstructed the jaw outline from the holotype, compared the material with both the Dvinosauridae and the Brachyopidae but did not attempt a definite allocation. As he noted, the reconstructed parabolic outline and the coronoid tooth row suggest *Dvinosaurus*. Brachyopid lower jaws were unknown at the time and direct comparisons with this family could not be made.

Boreosaurus thorslundi is a brachyopoid as Nilsson believed and a brachyopid as listed by Romer (1966). As in *Dvinosaurus primus* and *Bothriceps australis* the posterior meckelian foramen and the angular-prearticular suture are located low on the lingual surface.

Two details of construction provide evidence for the referral of *Boreosaurus thorslundi* to the Brachyopidae. The adductor fossa is long and narrow and the entire jaw is very slender, specifically recalling the jaws of *Blinasaurus henwoodi* rather than those of *Dvinosaurus primus*. Impressions of reticulate sculpture associated with the paratypes of *Boreosaurus thorslundi* lend circumstantial support for this assignment. The retroarticular process of the holotype, broken off close to its base, was probably elongate as in other brachyopids rather than short and knob-like as in *Dvinosaurus primus*.

One feature of lower jaw construction indicates closer relationship of *Boreosaurus thorslundi* to the Lower Triassic *Blinasaurus henwoodi* than to the Upper Permian *Bothriceps australis*. The entire jaw ramus is bowed strongly upward in lingual view whereas in *Bothriceps australis* it is nearly straight from the symphysis to the region beneath the articular facet.

The comparatively large size of the adductor fossa of *Blinasaurus henwoodi* is the principal feature of this species which distinguishes it from *Boreosaurus thorslundi*. In the Australian species the greatest length of this fossa is 0.41 of the length of the lower jaw from the symphysis to the anterior edge of the articular facet. The same index for the Spitsbergen species is 0.25. The labial wall of the fossa is much higher in *Blinasaurus henwoodi* than it is in *Boreosaurus thorslundi*. The posterior meckelian foramen and angular-prearticular suture lie closer to the ventral edge of the jaw in *Blinasaurus henwoodi* than in *Boreosaurus thorslundi*. The posterior meckelian foramen of *Blinasaurus henwoodi* is relatively smaller.

Boreosaurus thorslundi is the first known occurrence of a true brachyopid in the European region. As such, it is of considerable palaeographic interest. Brachyopid distribution, formerly believed to be limited to the equatorial and austral regions, is now known to have included the northern continents. The family is represented in North America by *Hadrokkosaurus bradyi* and in Spitsbergen by *Boreosaurus thorslundi*.

Batrachosuchus watsoni Haughton, 1925. This is the more fully described and illustrated of two species of the genus. The holotype and only specimen, B.M.N.H. no. R3589, is a complete skull prepared on all surfaces, which was first described by Watson (1919, p. 44, figs. 27 and 28, pl. I) as *Batrachosuchus* sp. Haughton (1925, p. 257) provided the species name, *Batrachosuchus watsoni*. A revised description with new illustrations was contributed by Watson (1956, p. 331, figs. 5, 6, 7, 33D and 34D). The skull was collected from an unknown locality in the *Cynognathus* zone in the Burghersdorp district of South Africa.

Three features of the skull indicate that this species is more closely related to the species of *Blinasaurus* than it is to *Bothriceps australis*, *Trucheosaurus major* and *Brachyops laticeps*. The snout region has a broadly parabolic outline in dorsal view as in the species of *Blinasaurus* and not slightly pointed as in the other species. The subtemporal fossae are long and narrow as in *Blinasaurus henwoodi* and lack the medial indentations by projecting processes of the pterygoids observed in *Bothriceps australis*. The level of the quadrate condyles is far anterior to the level of the exoccipital condyles as in both species of *Blinasaurus* whereas in *Bothriceps australis* the quadrate and exoccipital condyles are nearly on the same hinge line. Each of the exoccipital-pterygoid sutures visible on the palatal surface of the *Batrachosuchus watsoni* skull is nearly 2 cm in length and in this respect also the species is much closer to *Blinasaurus henwoodi* than it is to *Bothriceps australis*.

The principal features that distinguish *Batrachosuchus watsoni* from the species of *Blinasaurus* are the position of the orbits on the skull roof and the arrangement of the canals of the lateral line system. The orbits are widely spaced in the anterior part of the skull. The length of the preorbital region measured on the midline and the least interorbital width are 0.20 and 0.46 respectively of total skull roof midline length. The latter index is close to those determined for *Brachyops laticeps* and *Trucheosaurus major*. The relative size of the orbit is close to that of *Blinasaurus wilkinsoni* but less than that of *Blinasaurus henwoodi*. The greatest length of the orbit is 0.23 of skull roof midline length.

In regard to the lateral line system the major difference between *Batrachosuchus watsoni* and the species of *Blinasaurus* is the course of the supraorbital canal in the postorbital region. This canal, in *Batrachosuchus watsoni*, does not join the infraorbital and temporal canals in the postorbital bone. Instead, it curves medially behind the level of the posterior border of the

orbit and ends blindly in the parietal bone. The species of *Blinasaurus*, however, resemble *Bothriceps australis*, *Brachyops laticeps* and most other temnospondyl species in possessing confluent supraorbital, infraorbital and temporal canals in the postorbital bones.

A number of features of the palatal surface distinguish *Batrachosuchus watsoni* from *Blinasaurus henwoodi*. The interpterygoid vacuities are relatively smaller with a distinctive outline. The greatest length of each vacuity is 0.52 of total midline length of the dorsal surface whereas in *Blinasaurus henwoodi* this index is 0.63. The anterolateral "corner" of each vacuity is on the same level as the anteromedial "corner" whereas in *Blinasaurus henwoodi* the anterolateral "corner" is posterior to the anteromedial "corner". The cultriform process lacks a waist in the centre of its length. The vomerine tusks are considerably smaller than the palatine husks and not equal to them in size as in *Blinasaurus henwoodi*.

Batrachosuchus browni Broom, 1903. This is the type species of the genus and is also based on a single skull. This skull, housed in the South African Museum, Capetown, was found at Aliwal North, Cape Province, South Africa and is "presumably from the *Cynognathus* zone" (Watson, 1956, p. 322).

Broom's (1903, p. 499, figs. 1 and 2) original account was supplemented by Watson (1919, p. 47 and 1956, p. 336, figs. 8 and 32D). The species is very close to *Batrachosuchus watsoni* in most of its important characters including the position of the orbits on the skull deck, the course of the supraorbital canal, the length of the exoccipital-ptyergoid suture, the shape of the cultriform process, and the outlines of the interpterygoid vacuities and subtemporal fossae. Watson (1956, p. 336) provided the specific characters, noting the "greater projection of the occipital condyles behind the occipital border of the skull roof" and the fact that: "The lateral line grooves have the same general distribution as in *B. watsoni*, but are actually and relatively much narrower and of more U-shaped section." Watson (loc. cit.) also distinguished the species by stating that the orbits of *Batrachosuchus browni* are further back. This distinction, however, is open to question. Measurements taken from Watson's (1956, fig. 8) illustration give an index of 0.20 for the preorbital length of the skull roof whereas this index is 0.23 in *Batrachosuchus watsoni*, based on measurements from the actual skull.

Hadrokkosaurus bradyi (Welles, 1947). The species was originally described as *Taphrognathus bradyi* (Welles, 1947, p. 246, Figs. 3-10) but the generic name was found to be preoccupied and was changed to *Hadrokkosaurus* (Welles, 1957, p. 982). The holotype, U.C.M.P. no. 36199, is a nearly complete right ramus of a lower jaw found at U.C.M.P. locality V3922, a quarry in the Holbrook member of the Moenkopi Formation six miles west of Holbrook, Arizona.

Drs. S. P. Welles and R. D. Estes are currently reviewing the species and, in a forthcoming report, will comment on the holotype and various topotypic material and describe a well-preserved

skull from the Holbrook Member near Cameron, Arizona.

Welles (1947) placed "*Taphrognathus*" *bradyi* in the Plagiosauridae, citing as characters several features that are also similar to those in the Brachyopidae: the parabolic curvature of the lower jaw; its large teeth and short tooth row; and the extensive retroarticular process. The detailed construction of the lower jaw, however, serves to place *H. bradyi* in the Brachyopidae rather than the Plagiosauridae. In labial view (Welles, 1947, Fig. 3a) the ventral edge of the jaw is bowed slightly upward under the tooth row and, again, under the articular facet. The lingual wall of the adductor fossa is much lower than the labial wall. The posterior meckelian foramen and angular-prearticular suture, although not on the ventral surface, are placed very low on the lingual surface.

Two features of the labial surface of the lower jaw are unique to *Hadrokkosaurus bradyi* among the Brachyopidae: the external surfaces are devoid of sculpture; and a large lateral mandibular fenestra is present between the dentary and surangular bones.

Hadrokkosaurus bradyi is also distinguished from *Blinasaurus henwoodi* by the same features which distinguish *Boreosaurus thorslundi*. The adductor fossa is relatively shorter, the greatest length of this opening being 0.33 of the length of the outside curvature of the jaw from the symphysis to the anterior edge of the articular facet. The same index for *Blinasaurus henwoodi* is 0.41. The posterior meckelian foramen is relatively larger.

Evolution of the Brachyopidae

Watson (1919, pp. 56-57) cited three trends in structural modification that have occurred in the evolution of the brachyopid skull. Successive stages in this evolution were marked by the late Permian genera *Dvinosaurus* and *Bothriceps*, the early Triassic *Batrachosuchus* and the Late Triassic *Plagiosaurus*. Although *Plagiosaurus* and its allies are now removed to a separate order (Panchen, 1959) or suborder (Romer, 1966), the trends noted by Watson still apply to the other genera.

(1) The series shows a progressive movement forward on the quadrate condyles from a position level with the hinge line of the exoccipital condyles to an anterior position.

(2) The exoccipital and pterygoid bones do not meet in *Dvinosaurus*. There is a short suture between these elements in *Bothriceps* and a wide suture in *Batrachosuchus*.

(3) In *Bothriceps* the hypoglossal foramen is on the lateral surface of the exoccipital. In *Batrachosuchus* it is on the posterior surface of the bone directly above the condyle.

Blinasaurus henwoodi is at the same level of development as *Batrachosuchus*. The hinge lines of the quadrate condyles are anterior to the exoccipital condyles and the exoccipital-ptyergoid sutures are well developed.

Watson (1956) has also noted an increase through time in the size of the retroarticular process of the lower jaw. This is substantiated by a comparison of the retroarticular process of

Bothriceps with those of *Blinasaurus* and *Hadrokkosaurus*. The process of *Bothriceps* is 0.10 of the total length of the lower jaw from symphysis to the tip of the retroarticular process (as measured along the outside curvature). The quotients for *Blinasaurus* and *Hadrokkosaurus* are 0.16 and 0.18 respectively. Lower jaw fragments of *Batrachosuchus* in the U.C.M.P. collections indicate that the retroarticular process of this genus was also comparatively large.

The Early Triassic genera, *Batrachosuchus*, *Blinasaurus*, and *Hadrokkosaurus* share a number of characters that distinguish them from Late Permian genera, best exemplified by *Bothriceps*. To Watson's summaries I would add the following changes that occurred in Late Permian and Early Triassic time:

(1) The skull has lost the triangular outline of *Bothriceps* and *Trucheosaurus* and become more nearly circular in the Early Triassic genera. *Brachyops* is intermediate in this respect.

(2) The subtemporal fossa of *Bothriceps* is shorter and wider than those of *Batrachosuchus*, *Blinasaurus* and *Hadrokkosaurus*. A projection of the palatal ramus of the pterygoid, lacking in the Triassic genera, indents the lateral margin of the fossa in *Bothriceps*.

(3) The lower jaw ramus of *Bothriceps* is deep in the region between the adductor fossa and the symphysis and comparatively shallow in *Blinasaurus*, *Boreosaurus* and *Hadrokkosaurus*.

The modifications of the brachyopid cranium in Late Permian and Early Triassic time signify an improvement in the power and manoeuvrability of the jaw mechanism. The broadening and rounding of the skull has, in turn, shortened the gape. The elongation of the subtemporal fossa provides an increased area of attachment for the adductor muscles. With these structural changes the jaws of Triassic brachyopids could be brought together with considerably greater pressure than could the jaws of *Bothriceps*. The lengthening of the retroarticular process provides an increased area of insertion for the muscles which open the jaws and, with the greater leverage thus obtained, the jaws of Triassic genera could be swung open more rapidly.

The brachyopids were probably an aquatic, piscivorous group. The structural changes in the jaws of the later genera suggest a trend towards increasing predaceousness and perhaps a concentration on larger prey. This concept is supported by the increase in size of the palatal tusks in *Blinasaurus* and *Batrachosuchus* over those of *Bothriceps*.

Remarks on some problematic species of the Amphibia

Tungussogyrinus bergi Efremov, 1939, is known from a larval amphibian skeleton from the Triassic of the Tungus basin, Siberia, which includes part of the palatal skull surface, a left lower jaw, a series of twenty-odd articulated vertebrae, most of the left forelimb and a left ilium and femur. Romer (1966) considered it a possible member of the Brachyopidae.

Positive assignment is impossible. The construction of the quadrate region, crucial for comparisons with the Brachyopidae, is unknown. The skull apparently lacks the high vault of the posterior part of the palate which is characteristic of the brachyopoids, and the exceptionally broad cultriform process and the solid, elongate vertebral centra suggest the Plagiosauria. The short broad skull, the broad cultriform process, and the forward positions of the orbits and quadrate condyles and possibly larval features as Efremov has pointed out.

Indobrachyops panchetensis Huene and Sahni, 1958 is a short-snouted labyrinthodont based on an incomplete skull from the Lower Triassic Panchet series of India.

The rudimentary otic north of *I. panchetensis* recalls the Brachyopidae but in other respects the Indian species is quite different. The occipital condyles lie closer to the posterior margin of the skull roof. The cheek region is shallow and the peculiar brachyopid modifications of the pterygoid, squamosal and quadratojugal are not present.

The sculpture of *Indobrachyops* consists of irregular vermiculose ridges and bears little resemblance to either the lineate sculpture of *Dvinosaurus* or the reticulate pattern of the Brachyopidae. The skull, although broad and short, has a different shape from a brachyopid skull. The brachyopid skull has a bulging cheek region and the greatest width of the skull lies anterior to the posterior corners. *Indobrachyops* has straight cheek margins and the greatest width lies at the posterior corners.

Indobrachyops possesses several features of the skull that recall the Rhytidosteidae. The orbits are near the centres of the lateral margins of the skull and the parietal foramen lies close behind a line connecting the posterior borders of the orbits. The cultriform process is broad and shagreen is present on the pterygoid and ectopterygoid bones.

Several important differences prevent the inclusion of *Indobrachyops* in the Rhytidosteidae. The sculpture pattern is quite different. The external nares, set close together in *Indobrachyops*, are widely separated in *Deltasaurus* and *Rhytidosteus*. The lacrimal bone, entirely lacking in rhytidosteids, is large in *Indobrachyops* and has an extensive border on the orbit.

The similarities to the Rhytidosteidae are perhaps parallelisms indicating a common origin with this family among the Rhinesuchoidea of the Upper Permian. For the present *Indobrachyops* should be listed as *incertae sedis* among the superfamilies of Temnospondyli.

Tupilakosaurus heilmani Nielsen, 1954. The type material is a disarticulated assemblage of bones scattered through a shale slab from the Lower Triassic deposits of the Kap Stosch area, Eastern Greenland. Among the remains are a central fragment of a skull roof and a number of pleurocentra and intercentra from an embolomeric vertebral column.

Nielsen (1954), followed by Von Huene (1956) concluded that *T. heilmanni* was an embolomereous trematosaur and that it represented an evolutionary stage ancestral to the ichthyosaurs. Von Huene (1959) again noted the features that resemble those of both the Embolomeri and the Trematosauridae but stated that it was impossible to prove the ichthyosaurian affinities of the species on the basis of the known material.

Shishkin (1961), partly from observations on the material discussed below under *Tupilakosaurus wetlugensis*, concluded that the skull fragment of *T. heilmanni* was derived from a broad-skulled labyrinthodont of the superfamily Brachyopoidae. He made the genus the type of a new family, Tupilakosauridae, and accepted the embolomereous vertebrate as derived from the same skeleton as the skull fragments. Romer (1966) placed the species in the Brachyopoidae.

Prompted by Shishkin's interpretation, Nielsen (1967) accomplished further preparation on the shale slab, exposing the dorsal surface of the skull fragment and uncovering a number of additional skeletal elements. The dorsal aspect of the skull fragment confirms its brachyopoid nature but is too incomplete by itself for extensive comparisons with other species of the superfamily.

Tupilakosaurus wetlugensis Shishkin, 1961. The species is based on a nearly complete skull of a brachyopoid labyrinthodont and some embolomereous pleurocentra and intercentra from near Spasskoye Village on the Vetluga River, European Russia. The locality lies within zone V of the Cis-Uralian continental sequence.

The generic assignment rests on the similarity of the central elements to those preserved on the shale slab with the indeterminate skull fragments of *T. heilmanni*. The association of such vertebrae with a temnospondylous skull is as suspect in this case as it is in the Greenland occurrence. Shishkin does not indicate if the vertebrae were found articulated with the skull or even in close proximity to it. Moreover, the occurrence of embolomereous vertebrae in a brachyopoid would be anomalous as all members of the superfamily for which vertebral structures are known, are temnospondylous. Large, wedge-shaped intercentra occur in *Dvinosaurus primus* (Bystrov, 1935, Fig. 26), in undescribed *Batrachosuchus* material in the U.C.M.P. collections and in new, undescribed brachyopoid material from Tasmania.

The skull of *Tupilakosaurus wetlugensis* (Shishkin, 1961, Figs. 1 and 2) is clearly that of a brachyopoid. Otic notches are lacking. The cheeks are downturned and the occipital structures slope down and back from the posterior edge of the skull roof.

Many features of the skull of *T. wetlugensis* closely resemble those of *Dvinosaurus primus* (Bystrov, 1938, Figs. 1, 5-10, 21-25). The anterior end of the cultriform process has a pronounced expansion between the enclosing wings of the vomers in *T. wetlugensis* as in *D. primus*. Both genera possess vestiges of a palatal tooth row. In *T. wetlugensis* there are two teeth of

this row on the palatine bone behind the tusk, two in front of the tusk on the ectopterygoid bone and six more behind the ectopterygoid tusk. In *D. primus* there are five teeth of this row on the ectopterygoid behind the tusk and five more between the palatine and vomerine tusks along the medial border of the choana. Although most brachyopoids lack teeth of the palatal tooth row in the posterior part of the mouth, *Batrachosuchus watsoni* (Watson, 1956, Fig. 6) and an undescribed *Blinasaurus* skull from Tasmania possess transverse rows of small teeth on the vomer bones just behind the snout tip but there are no traces of small teeth on the medial borders of the choanae or between the large tusks of the palatine and ectopterygoid bones.

The arrangement of bones and lateral line grooves on the dorsal surfaces of the skulls is very similar in the two genera. The parietal bones have lateral borders on the postorbital bones on the *T. wetlugensis* skull and on one specimen of *D. primus*. The orbits in both genera are spaced moderately far apart.

The most notable difference between *T. wetlugensis* and *D. primus* is in the structure of the basicranial region of the palate. *D. primus* possesses the movable joints of the central parasphenoid-basisphenoid complex with the lateral pterygoid bones found in *Eobrachyops* and other Early Permian genera but in *T. wetlugensis* the parasphenoid is solidly fused to the pterygoids. If *T. wetlugensis* is a Triassic descendant of the Late Permian *Dvinosaurus* then this lineage has paralleled that of the brachyopoids and other labyrinthodont families in the loss of the basipterygoid joints.

Stratigraphic relationships

The stratigraphic position of the fauna from the Blina Shale lies close to the base of the Triassic System, a determination that rests on a correlation of the vertebrate-bearing portion of this unit with a vertebrate horizon in the Kockatea Formation of the Perth Basin in southwestern Western Australia (see Cosgriff, 1965, pp. 88-89). The correlation is founded on both vertebrate and palynological evidence. The rhytidosteid genus, *Deltasaurus*, is represented in the Blina Shale by *D. kimberleyensis* and in the Kockatea Formation by *D. pustulatus*. These horizons both contain the *Taeniosporites* microfloral assemblage (Balme, 1963, pp. 36-37). The horizon in the Kockatea Formation, in addition, contains a marine invertebrate assemblage composed of ammonites and bivalves. Dickens and McTavish (1963) have concluded from an analysis of these that the horizon lies within the Otoceratan Division which is the basal portion of Spath's (1935) sequence for the Scythian Stage. By inference, therefore, the fauna from the Blina Shale is also basal Triassic in position and probably lies within the Otoceratan Division.

Vertebrate and palynological evidence provides a correlation of the vertebrate faunal horizon in the Knocklofty Formation of Tasmania (noted in the introduction) with the vertebrate faunal horizon in the Blina Shale. *Deltasaurus*

kimberleyensis and closely related species of *Blinasaurus* are present in both faunas. The faunas also share material referable to the fish genera *Ceratodus* and *Saurichthys* but these taxa are not useful in stratigraphy. Two diagnostic species of the microflora in the vertebrate horizon of the Kockatea Formation have been identified in a pollen sample taken from a level in the vertebrate horizon of the Knocklofty Formation at Crisp and Gunn's Quarry, Hobart (G. Playford, pers. comm. to M. R. Banks; see Banks and Naqvi, 1967, p. 26). These species, *Lundblattispora brevicula* and *Densoisporites playfordi*, thus serve to strengthen the correlation of the Triassic vertebrate horizon of Tasmania with those of Western Australia and to tentatively assign it a position in the Otoceratan Division of the Scythian Stage.

The standard reference for stratigraphic correlations of Early Triassic vertebrate faunas has been the upper part of the Beaufort Series, Karroo System of South Africa. This unit contains two distinct faunal horizons, the *Lystrosaurus* zone at the base and the *Cynognathus* zone at the top (Hotton and Kitching, 1963). Romer (1947 and 1966) correlated the vertebrate faunas from the Mangali and Panchet beds of India and Zone V (Vetlugian) of the Cis-Uralian continental sequence of the U.S.S.R. with the *Lystrosaurus* zone, the major taxonomic base for the correlations being the occurrence in most of the faunas of closely related erythrosuchid and lystrosaurid reptiles. He correlated the vertebrate faunas from the Bunter Series of Western Germany and Zone VI of the Cis-Uralian sequence with the *Cynognathus* zone, the principle taxonomic basis being the occurrence in all faunas of species of the capitosaurid genus, *Parotosaurus*. Another fauna containing a *Parotosaurus* species which may be included in this stratigraphic interval is the one from the Wupatki member of the Moenkopi Formation of Arizona (Welles and Cosgriff, 1965).

Unfortunately the faunas from the *Lystrosaurus* and *Cynognathus* zones and those from all of the correlated deposits are not associated with ammonites or other marine invertebrates. Thus, there is no direct means by which they may be related to the marine stratigraphic sequence. Romer (1947) placed the *Lystrosaurus* zone and its equivalents in the Lower Scythian and the *Cynognathus* zone and its equivalents in the Upper Scythian. These assignments were questioned by the author (1965) on the basis of the new stratigraphic evidence derived from the Blina Shale and Kockatea Formation. The vertebrate fossil horizons of both of these Formations were correlated with the *Cynognathus* zone on the close similarity of the species of *Deltasaurus* with *Rhytidosteus capensis*. Inasmuch as the Western Australian fossil horizons lie at the very base of the Triassic System it was conceived that the *Cynognathus* zone was also basal Triassic and that the *Lystrosaurus* zone was Upper Permian.

This interpretation, however, must now be slightly modified owing to the new stratigraphic evidence provided by the vertebrate fauna from

Tasmania. This fauna contains two forms which suggest a correlation with the *Lystrosaurus* zone: a new lydekkerinid which is close to *Lydekkerina huxleyi* and *Limnoiketes paludinatans*; and a new chasmatosaurid which is close to *Chasmatosaurus vanhoepeni*. *Deltasaurus kimberleyensis* and *Blinasaurus* sp., however, tend to relate the fauna to the *Cynognathus* zone through their similarities to *Rhytidosteus capensis* and the species of *Batrachosuchus*. Although these few taxonomic relationships constitute a very tenuous basis for stratigraphic correlations they suggest an intermediate position for the vertebrate faunal horizon in the Knocklofty Formation (and also for those in the Western Australian units) between the *Lystrosaurus* zone and the *Cynognathus* zone. Since the Tasmanian fauna and its Western Australian correlates are either within or close to the Otoceratan Division the *Cynognathus* zone and its correlatives would be farther up in the Triassic System. The author's previous interpretation of the *Lystrosaurus* zone as an Upper Permian horizon (Cosgriff, op. cit.) remains unchanged.

Three lines of evidence clearly indicate that the vertebrate fauna from the Gosford Formation of New South Wales which contains *Blinasaurus wilkinsoni* is stratigraphically above the faunal horizons of the Blina, Kockatea and Knocklofty Formations and that it is close in position to the *Cynognathus* zone:

(1) An undescribed species of *Parotosaurus* mentioned in the introduction, is associated with *Blinasaurus wilkinsoni* in the fauna from Gosford. *Parotosaurus* occurs in the *Cynognathus* zone of South Africa but is not present in the *Lystrosaurus* zone. It is also widely distributed around the world, furnishing correlations with the *Cynognathus* zone for the faunas from the Wupatki Member of the Moenkopi Formation of Arizona (Welles and Cosgriff, 1965), the Bunter Series of Western Germany and Zone VI of the Cis-Uralian sequence of the U.S.S.R. (Konzhukova, 1965). Parenthetically it should be noted here that the fish component of the Gosford Fauna is of little stratigraphic value; all of the recognized taxa are either long-ranging, poorly-known or endemic forms.

(2) Townrow (1966) has commented on a fossil leaf flora from a locality at Turrismetta Head in New South Wales which lies near the top of the Narrabeen Group. This flora is taxonomically close to that from a locality in the *Cynognathus* zone at Brown's River, South Africa. Both floras contain *Lepidopteris madagascariensis* and abundant material of the genus *Dicroidium*. The flora from Turrismetta Head is probably close in time to the fauna from the Gosford locality as it too lies near the top of the Narrabeen Group. However, there are no available data to provide a direct correlation.

(3) Palynological evidence also indicates that the fauna from Gosford is stratigraphically higher than the Western Australian and Tasmanian faunas. A microfloral assemblage containing the pollen *Pteruchipollenites* is widespread through the Narrabeen Group, occurring

even in its lower 75 feet (Hennelly, 1958). Balme (1963) states that this same assemblage, which is quite different from the *Taeniosporites* assemblage, occurs above the latter in the Kockatea Formation and is also found in the Erskine Formation which directly overlies the *Taeniosporites*-containing Blina Shale in the Fitzroy Trough. He concludes that, although a possibility remains that the *Taeniosporites* and *Pteruchipollenites* assemblages represent different but contemporary floral facies, it is more likely that they are time-sequential. He further notes that the absence of the *Taeniosporites* assemblage in the Triassic sequence of the Sydney Basin suggests that the lowermost portion of the system is not present here.

Two of the brachyopid species discussed in this report, *Trucheosaurus major* and *Brachyops laticeps* are older than *Blinasaurus henwoodi* and five, *Batrachosuchus browni*, *Batrachosuchus watsoni*, *Blinasaurus wilkinsoni*, *Boreosaurus thorslundi* and *Hadrokkosaurus bradyi* are younger. The provenance of *Bothriceps australis*, as noted earlier, is uncertain but it is believed to have been collected from the Lithgow Coal Measures of New South Wales, the deposits that produced *Trucheosaurus major*. The stratigraphic position of *Boreosaurus thorslundi* in the marine scale for the Triassic is established by associated invertebrate fossils. A lower limit for the occurrence of *Hadrokkosaurus bradyi* relative to the marine scale is set by marine fossils which occur below its faunal level in the Moenkopi Formation. The occurrences of the remaining species may be plotted only on the stratigraphic scale provided by fossil vertebrate zones in the Beaufort Series of South Africa. The range of this scale relative to the marine scale is uncertain. As indicated earlier in this discussion, the vertebrate fauna from the Knocklofty Formation appears to be above the *Lystrosaurus* zone but below the *Cynognathus* zone. The close taxonomic relationships of this fauna to both of the African zones suggests that they follow each other closely in time in the sequence: *Lystrosaurus* zone—Knocklofty Formation fauna—*Cynognathus* zone. This would infer that the *Lystrosaurus* zone lies just below the Permo-Triassic boundary and the *Cynognathus* zone lies in one of the divisions of the Scythian Stage following the Otoceran. With this composite continental-marine standard in mind the evidence for the stratigraphic positions of the various brachyopid species, from the oldest to the youngest is summarized as follows:

Trucheosaurus major (and *Bothriceps australis*?). The *Glossopteris* flora occurring in the Lithgow Coal Measures which produced the first and possibly the second of these two species indicates an Upper Permian position (David, 1950). The slightly triangular outline of the skulls of these species, considered to be a primitive feature, is more pronounced in these species than in the next form considered.

Brachyops laticeps. The horizon in the Mangali beds of Central India which produced this species is probably homotaxial with the *Lystrosaurus* zone of the Beaufort Series. This is in-

ferred by floral similarities between these beds and the Panchet beds of Bengal (von Huene, 1942). The Panchet beds contain a vertebrate fauna which includes a species *Lystrosaurus* (Robinson, 1958), a taxon that directly correlates it with the *Lystrosaurus* zone.

Boreosaurus thorslundi. This is the only brachyopid species that occurs in a rock unit containing diagnostic invertebrate fossils and is, thus, the only one that may be assigned a position in the marine sequence on direct stratigraphic evidence. The Upper *Posidonomya* beds or "Fish Horizon" (Frebald, 1930) of Spitsbergen contain a mixed marine-continental fossil assemblage which includes ammonites, bivalves, a large variety of fish, several trematosaurid temnospondyls and *B. thorslundi*. These beds have been included in the Sticky Keep Formation by Buchan *et al* (1965). Kummel (1961) reexamined the arctoceratid ammonites from the faunal horizon and, on the basis of these, assigned the Upper *Posidonomya* beds to Spath's (1934) Owenitan Division of the Scythian Stage.

Batrachosuchus browni, *Batrachosuchus watsoni* and *Blinasaurus wilkinsoni*. As shown above, the last species from the Gosford Formation appears to be a close contemporary of the first two from the *Cynognathus* zone of the Beaufort Series. Stratigraphic evidence for assigning the *Cynognathus* zone fauna, the Gosford Formation fauna and their various equivalents around the world an exact position in the marine sequence is completely lacking. Data from the Moenkopi Formation of Arizona and Utah, however, served to place a tentative lower limit on the stratigraphic occurrence of this complex of faunas. McKee (1954) examined and compared two sections of the Moenkopi Formation, one in southeastern Utah and one along the Little Colorado River in Arizona. The first of these is an alternating sequence of marine and continental units comprising, from bottom to top, the Lower Red Member, the Virgin Limestone, the Middle Red Member, the Shnabkaib Member and the Upper Red Member. The second section is entirely in a continental deposit including, from bottom to top, the Wupatki, Moqui and Holbrook Members. A fossil vertebrate fauna from the Wupatki Member includes *Parotosaurus peabodyi* (Welles and Cosgriff, 1965), a species close to *Parotosaurus haughtoni* from the *Cynognathus* zone and a new *Parotosaurus* from the Gosford Formation. A fauna from the Holbrook Member includes *Hadrokkosaurus bradyi*. From a consideration of intervening exposures, McKee (1954, fig. 8) concluded that the entire section along the Little Colorado is stratigraphically above the level of the Virgin Limestone of southeastern Utah. Further, he notes (1954, p. 75) that the Virgin Limestone contains diagnostic ammonites and quotes a personal communication from Muller (1951), "who states that they represent the *Tirolites* zone." This zone is part of Spath's (1934) Columbitan division of the Scythian. The faunas from the Wupatki and Holbrook Members are, therefore, Columbitan at the lowest and may represent portions of the Stephanitan or even of the Anisian and Ladinian

stages as well. It is unlikely that they lie as high as the Upper Triassic Karnian which is considered to be equivalent to portions of the lower part of the Keuper Group in Europe, deposits that contain distinctive Late Triassic vertebrate faunas.

Haddockosaurus bradyi. As noted above, this species is a component of a vertebrate fauna from the Holbrook Member of the Moenkopi Formation (Welles, 1947). This fauna also contains advanced capitosaurids with closed otic notches, forms which are clearly advanced over the genus *Parotosaurus* of the Wupatki Member, the Gosford Formation and the *Cynognathus* zone. The character of the fauna is thus in keeping with its superior stratigraphic position which may lie as high as the Ladinian. At any rate, *Haddockosaurus* is the youngest known brachyopid.

The known and suspected stratigraphic positions of the various brachyopid species in the Upper Permian, Lower Triassic and Middle Triassic are summarized in Table 2. This employs Spath's (1935) arrangement of divisions for the Scythian but does not employ formal subdivisions for the Upper Permian owing to the lack of agreement among authorities concerning faunal and floral sequences during this interval.

TABLE 2

Middle Triassic		? <i>Batrachosuchus browni</i> ? <i>Batrachosuchus watsoni</i> ? <i>Blinasaurus wilkinsoni</i> ? <i>Haddockosaurus bradyi</i>
Lower Triassic = Scythian	Stephanitan	
	Columbitan	
	Owenitan	<i>Boreosaurus thorslundi</i>
	Flemingitan	
	Gyronitan	
	Otoceratan	<i>Blinasaurus henwoodi</i> , <i>Blinasaurus</i> sp.
Uppermost Permian	<i>Brachyops laticeps</i>	
Upper Permian	<i>Trucheosaurus major</i> , ? <i>Bothriceps australis</i>	

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References

- Balme, B. E. (1963).—Plant microfossils from the Lower Triassic of Western Australia. *Palaeontology* 6(1): 12-40.
- Banks, M. R. and Naqvi, I. H. (1967).—Formations close to the Permo-Triassic Boundary in Tasmania. *Pap. Proc. R. Soc. Tasm.* 101: 17-30.
- Broom, R. (1903).—On a new stegocephalian (*Batrachosuchus browni*) from the Karoo beds of Aliwal North, South Africa. *Geol. Mag.* (4)X: 499-501.
- (1915).—On the Triassic stegocephalians *Brachyops*, *Bothriceps* and *Lydekkerina*, gen. nov. *Proc. Zool. Soc. London*, 1915: 363-368.
- Brunnschweiler, R. O. (1954).—Mesozoic stratigraphy and history of the Canning Desert and Fitzroy Valley, Western Australia. *J. geol. Soc. Aust.* 1: 35-54.
- Buchan, S. H., Challinor, A., Harland, W. B. and Parker, J. R. (1965).—The Triassic stratigraphy of Svalbard. *Skript. Norsk. Polarinst.* 135: 1-94.
- Bystrov, A. P. (1935).—Morphologische Untersuchungen der Deckknochen des Schädels der Wirbeltiere I Mitteilung. Schadel der Stegocephalen. *Acta Zool., Stock.* 16: 65-141.
- (1938).—Dvinosaurus als neotenische Form der Stegocephalen. *Acta Zool., Stock.* 19: 209-295.
- Case, E. C. (1946).—A census of the determinable genera of the stegocephalia. *Trans. Am. Philos. Soc.* 35: 325-420.
- Cosgriff, J. W. (1965).—A new genus of Temnospondyli from the Triassic of Western Australia, *J. R. Soc. W. Aust.* 48(3): 65-90.
- David, T. W. E. (1950).—*The Geology of the Commonwealth of Australia*. Edward Arnold & Co. London. 3 vols.
- Dickins, J. M. and McTavish, R. A. (1963).—Lower Triassic marine fossils from the Beagle Ridge (B.M.R. 10) Bore, Australia. *J. geol. Soc. Aust.* 10(1): 123-140.
- Efremov, J. A. (1928).—(Contributions to the Permo-Triassic fauna of the Volga-Dvinian variegated beds). *Proc. Third Cong. Russ. Zoolog. Anatom. Histolog., Leningrad*, 1927 (1928): 116-117.
- (1932).—On the Permo-Triassic labyrinthodonts of the Campylian beds of Mount Bolghoi Bogdo. II. On the morphology of *Dvinosaurus*. *Trav. Inst. Pal. Acad. Sci. URSS* 1, 1931(1932): 57-67.
- (1939).—First representatives of Siberian early Tetrapods. *C. R. Acad. Sci. URSS*, n.s. 23: 106-110.
- Frebold, H. (1930).—Die Altersstellung des Fischhorizontes, des Grippianireaus und des unterer Saurierhorizontes in Spitzbergen. *Skript. om Svalbard og Ishavet.* 28: 1-36.
- Guppy, D. J., Lindner, A. W., Rattigan, J. H. and Casey, J. N. (1958).—The Geology of the Fitzroy Basin, Western Australia. *Bull. Bur. Miner. Resour. Aust.* 36: 1-116.

- Haughton, S. H. (1925).—Investigations in South African fossil reptiles and Amphibia. 13. Descriptive catalogue of the Amphibia of the Karroo System. *Ann. S. Afr. Mus.* XXII: 227-261.
- Hennelly, J. B. F. (1958).—Spores and pollens from a Permian-Triassic transition, New South Wales. *Proc. Linn. Soc. N.S.W.* 83: 363-369.
- Hotton, N. and Kitching, J. W. (1936).—Speculations on Upper Beaufort deposition, *S. Afr. Jour. Sci.* 59(5): 254-258.
- Hills, E. S. (1958).—A brief review of Australian Fossil Vertebrates. Studies on Fossil Vertebrates Presented to D. M. S. Watson. T. S. Westoll, ed., Univ. of Lond, Athlone Press: 86-107.
- Huene, F. von (1922).—Beitrage zue Kenntnis der Organisation einiger Stegocephalen der schwabischen Trias. *Acta Zool.* III: 395-460.
- (1942).—Die Fauna der Panchetschichten in Bengalen. *Zentralbl. Min. Geol. Pal.* B(11): 354-360.
- (1948).—Short review of the lower tetrapods. *Roy. Soc. S. Afr. Spec. Publ. Robert Broom Comm. Vol.*: 65-106.
- (1956).—Palaontologie und Phylogenie der niederen Tetrapoden. *Jena: G. Fischer.*
- (1959).—Neucs uber *Tupilkosaurus*. *Neues. Jb. Geol. Paläont., Mh.*: 230-233.
- Huene, F. von and Sahni, M. R. (1958).—*Indobrachyops panchetensis* gen. et sp. nov. from the Upper Panchets. *Pal. Soc. India, Monogr.* 2: 1-17.
- Huxley, T. H. (1859).—On some amphibian and reptilian remains from South Africa and Australia. *Q. Jl. geol. Soc. Lond.* 15: 642-649.
- (1865).—Indian pre-Tertiary Vertebrata. On a collection of vertebrate fossils from the Panchet rocks near Ranigung, Bengal. *Pal. Indica* (4)1(1): 1-24.
- Jaekel, O. (1914).—Über die Wirbeltierfunde in der oberen Trias von Halberstadt. *Pal. Zeitschr.* 1: 155-215.
- Konzhukova, E. D. (1965).—(A new *Parotosaurus* from the Triassic of Cisuralia.) *Paleont. Zh.* 1: 97-104.
- Kummel, B. (1961).—The Spitsbergen arctoceratids. *Bull. Mus. Comp. Zool. Harvard* 123(9): 499-532.
- McKee, E. D. (1954).—Stratigraphy and history of the Moenkopi Formation of Triassic age. *Mem. Geol. Soc. Amer.* 61: 1-131.
- McKenzie, K. G. (1961).—Vertebrate Localities in the Triassic Blina Shale of the Canning Basin, Western Australia. *J. Roy. Soc. W. Aust.* 44 (3): 69-76.
- Nielsen, E. (1954).—*Tupilakosaurus heilmani*, n. g. et n. sp., an interesting batrachomorph from the Triassic of East Greenland. *Meddr. Grnland* 72(8): 1-33.
- (1967).—New observations on the skull-roof of the holotype of *Tupilakosaurus heilmani* Nielsen. *J. Linn. Soc. (Zool.)* 47(311): 225-229.
- Nilsson, T. (1943).—On the morphology of the lower jaw of Stegocephalia with special reference to Eotriassic stegocephalians from Spitsbergen. I. Descriptive part. *K. Svenska VetenskAkad. Handl.* (3)20(9): 1-46.
- (1946).—On the genus *Peltostega* Wiman and the classification of the Triassic stegocephalians. *K. Svenska VetenskAkad. Handl.* (3)23(3): 2-55.
- (1946a).—A new find of *Gerrothorax rhaeticus* Nilsson, a plagiosaurid from the Rhaetic of Scania. *Acta Univ. Lund* 42: 1-42.
- Owen, R. (1954).—Description of the cranium of a labyrinthodont reptile (*Brachyops laticeps*) from Mangali, central India. *Q. Jl. geol. Soc. Lond.* 10: 473-474.
- Panchen, A. L. (1959).—A new armoured amphibian from the Upper Permian of East Africa. *Phil. Trans. R. Soc. (B)*242(691): 207-281.
- Robinson, P. L. (1958).—Some new vertebrate fossils from the Panchet Series of West Bengal. *Nature* 182: 1722-1723.
- Romer, A. S. (1947).—Review of the Labyrinthodontia. *Bull. Mus. Comp. Zool. Harvard* 99: 3-352.
- (1966).—“Vertebrate Paleontology” (Chicago, Univ. Chicago Press).
- Säve-Söderbergh, G. (1935).—On the dermal bones of the head in labyrinthodont stegocephalians and primitive Reptilia with special reference to Eotriassic stegocephalians from East Greenland. *Meddr. Grnland* 98(3): 1-211.
- Shishkin, M. A. (1961).—(new data on *Tupilakosaurus*.) *Dokl. Akad. Nauk. SSSR* 136(4): 938-941.
- Spath, L. F. (1934).—The Ammonoidea of the Trias (I). *Cat. Fossil Cephalopoda Brit. Mus. (Nat. Hist.)*.
- (1935).—Additions to the Eo-Triassic invertebrate fauna of East Greenland. *Meddr. Grnland* 98(2).
- Stephens, W. J. (1887).—On some additional labyrinthodont fossils from the Hawkesbury sandstones of New South Wales. *Proc. Linn. Soc. N.S.W. (2)* I: 1175-1195.
- (1888).—On some additional labyrinthodont fossils from the Hawkesbury sandstone of New South Wales. Second note on *Platyceps wilkinsoni*. *Proc. Linn. Soc. N.S.W. Ser.* 2 II: 156-158.
- Sushkin, P. (1936).—Notes on the pre-Jurassic Tetrapoda from USSR. III. *Dvinosaurus Amalitzky*, a perennibranchiate stegocephalian from the Upper Permian of north Dvina. *Trav. Inst. Paleozool. Acad. Sci. URSS* 5: 43-91.
- Townrow, J. A. (1966).—On *Lepidopteris madagascariensis* Carpenter (Peltaspermaeae). *J. Proc. R. Soc. N.S.W.* 98: 203-214.
- Wade, R. T. (1940).—The Triassic fishes of Gosford, New South Wales. *J. Proc. R. Soc. New South Wales* 73: 206-217.
- Watson, D. M. S. (1919).—The structure, evolution and origin of the Amphibia. The “Orders” *Rachitomi* and *Sterospondyli*. *Philos. Trans. R. Soc. (B)* CCIX: 1-72.
- (1956).—The brachyopid labyrinthodonts. *Bull. Brit. Mus. (Nat. Hist.) Geology* 2(8): 315-391.
- Welles, S. P. (1947).—Vertebrates from the Upper Moenkopi Formation of northern Arizona. *Univ. Calif. Publ., Bull. Dept. Geol. Sci.* 27: 241-289.
- (1957).—New name for a brachyopid labyrinthodont. *J. Paleont.* 31(5): 982.
- Welles, S. P. and Cosgriff, J. W. (1965).—A revision of the labyrinthodont family Capitosauridae and a description of *Parotosaurus peabodyi* n. sp. from the Wupatki Member of the Moenkopi Formation of Northern Arizona. *Univ. Calif. Publ. Bull. Dept. Geol. Sci.* 54.
- Woodward, A. S. (1890).—The fossil fishes of the Hawkesbury series of Gosford, New South Wales. *Mem. Geol. Surv. N. S. Wales (Pal.)* 4: 1-55.
- (1909).—On a new labyrinthodont from the oil shale at Airly, New South Wales. *Rec. Geol. Surv. N.S.W. VIII*: 317-319.